INVESTIGATING DIET, DISTRIBUTION, AND GROWTH OF SILVER HAKE (*MERLUCCIUS BILINEARIS*) IN THEIR NORTHERNMOST EXTENT IN THE GULF OF ST. LAWRENCE

By

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Abstract

Changing ocean conditions are driving distribution shifts in many marine species on a global scale, which will have major ecological implications for marine environments. I investigated the recent trend of increased silver hake (*Merluccius bilinearis*) abundances within the Gulf of St. Lawrence to characterize their biology in their northernmost extent. I assessed the diet and distribution of silver hake, as well as the overlap between the diet and distribution of silver hake with those of two resident species, Greenland halibut (*Reinhardtius hippoglossoides*) and redfish (*Sebastes* sp.). Silver hake's diet in the Gulf was primarily benthic, with smaller contributions from pelagic prey than in diets reported along other parts of their range. Overlaps of diet and distribution between silver hake and the two highly abundant resident species were also high. I analyzed otoliths from the silver hake samples to investigate the age structure and growth of hake in the Gulf of St. Lawrence. Hake's age structure in the Gulf is similar to that of nearby regions where most individuals are age four or younger, while von Bertalanffy growth rates showed higher rates of growth and lower asymptotic lengths in the Gulf compared to hake from the Scotian Shelf and Northeast United States Shelf. My results provide some of the first descriptions of silver hake biology within the Gulf of St. Lawrence.

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1. Introduction and Overview

Global climate change has and will continue to exert significant influence on the functioning of both terrestrial and marine ecosystems, with marine ecosystems being predicted to face changes at much greater rates than terrestrial ecosystems (Hoegh-Guldberg and Bruno, 2010; Pinsky et al., 2013; IPCC, 2014). Climate change resulting from increasing concentrations of atmospheric carbon dioxide has been a major driver of humanity's cumulative impacts within the oceans, which have led to shifts in abiotic conditions (Halpern et al., 2015). Changes that have been attributed to anthropogenic climate change include: elevated and more variable ocean temperatures, increased concentrations of dissolved carbon dioxide, decreased ocean pH, and reductions in global ice cover (Doney et al., 2009; 2012). These changes further drive broad scale trends such as altered circulation patterns, increased freshwater and nutrient inputs from terrestrial sources, and changes in ocean productivity (Polovina et al., 2008; Collins et al., 2010). In tandem with natural modes of environmental variability such as multi-decadal oscillations, heterogeneity among regions means that some will likely experience changes that are much greater in magnitude than global averages (Sorte et al., 2010; Poloczanska et al., 2013).

Marine organisms are largely limited by the environment that they inhabit, and any changes in environmental conditions such as temperature, pH, and oxygen concentrations will have an impact on physiological functioning. For example, many species have environmental tolerances that fall within relatively narrow ranges

(Scott, 1982; Peck et al., 2014). These species are able to acclimatize to temperature conditions within these ranges but when temperatures exceed or fall below their thermal tolerances, they become stressed and physiologically depressed (Pörtner and Knust, 2007; Neuheimer et al., 2011). In the context of warming ocean conditions, some of the impacts brought about by rapid warming include elevated metabolic rates, decreased reproductive success, and reduced survivorship (Brodte et al., 2006; O'Connor et al., 2007; Donelson et al., 2010; Hoegh-Guldberg and Bruno, 2010). These individual impacts may result in observed responses at population levels, where the combined effects on survivorship could lead to the decline or extirpation of a species from a part of their range (Sunday et al., 2012; Comte and Olden, 2017).

However, warming may also create new habitable areas. These dynamic changes have resulted in distribution shifts in both terrestrial and marine species. Examples around the world have shown that organisms, ranging from terrestrial flora to relatively mobile aquatic species, have experienced changes in their geographic distribution, and that a majority of these shifts have included polewards expansions (Perry et al., 2005; Hickling et al., 2006; Sorte et al., 2010; Thomas, 2010). Studies have noted that observed shifts are largely driven by regional trends in temperature that result in mismatches between regional conditions and species' thermal tolerances (Sunday et al., 2012; Pinksy et al., 2013), and that shifts appear to be faster in marine systems than terrestrial systems (Sorte et al., 2010; Poloczanska et al., 2013). For marine taxa, increasing ocean temperatures at the warmest extent

of a species' range can create conditions where temperatures are too high to tolerate while at the poleward extent where conditions are colder, ranges may expand with warming. Overall, this can result in a net poleward movement of a species' range. In addition to poleward shifts, increased regional temperatures may also result in movement to greater depths, a response that provides another form of thermal refuge (Nye et al., 2009; Pinsky et al., 2013). Despite evidence that shifts can occur at fast rates in marine systems, species-specific rates of shift are widely variable, which is believed to relate to the biological characteristics and thermal tolerances of the different species (Perry et al., 2005; Sunday et al., 2015). Rates of range shifts have been found to be higher in short-lived species that mature rapidly than in species with longer lifespans, as short-lived species experience faster population turnover (Perry et al., 2005). In a separate study, Sunday et al. (2015) determined that factors relating to dispersal capacity such as swimming ability and omnivory also promote range expansions. Differing thermal tolerances of marine species are also important, where thermally "generalist" species with a wide range of tolerance are less likely to undergo drastic shifts in contrast to thermally "specialist" species with narrower tolerances (Day et al., 2018).

Predator-prey and competition interactions in various marine ecosystems can also play a role in influencing rates and outcomes of range expansions. For example, biotic resistance at a species' expanding range edge can limit their proliferation through interactions with pre-existing predators or competitors (Riley and Griffen, 2017). At the same time, reduced inter- and intra-specific interactions

can be beneficial for an expanding species. Fish species have been found to exhibit better body condition at range edges that is related to reduced densities (Gutowsky and Fox, 2012; Lopez et al., 2012). In addition, range expansions may provide spatial refuges for the expanding species from predators. The enemy-release hypothesis is typically discussed with regards to introduced species, but can also relate to drastic range expansions. It is apparent that range shifts are complex and vary from species to species, and potential impacts on regional ecosystems are difficult to anticipate.

Nonetheless, the investigation of distribution shifts through an ecosystem perspective is important, as asymmetry in species' responses to regional trends can result in altered and novel ecological assemblages. Similar to human-mediated biological invasions by non-native species, range expansions by a small number of species into newly habitable regions may create inter-specific interactions with resident species such as predator-prey, competition, and parasitic interactions; each of which may exacerbate the already significant impacts of climate change (Best et al., 2007; Zarnetske et al., 2012). Novel interactions between emerging species and resident species are likely to result in climate "winners" and "losers" (Sorte et al., 2010). For example, the northward expansion of European hake in the warming North Sea introduced competitive pressures for the resident saithe population, which share similar prey with hake. In conjunction with direct warming stressors, the expansion of European hake has likely contributed to the decline in saithe biomass (Cormon et al., 2016).

In addition to ecological impacts, the socioeconomic implications of distribution shifts in marine species will also be critical concerns as marine species represent an important source of income and nutrition for a major part of the world's population. The average annual per capita consumption of fish has increased steadily from 14.4 kg in the 1990s to over 20 kg by 2015 (FAO, 2016). Fish species are relatively more mobile than human populations, especially in the developing world, and as such distribution shifts and localized extinctions are likely to have severe consequences for populations that are less capable of adapting to the loss of their fisheries resources (Allison et al., 2009; Cheung et al., 2010). The economy of wealthier maritime communities will also feel the impacts of distribution shifts. Shifting stocks can result in fish harvesters having to travel further from their home ports, therefore spending more time and fuel in order to catch the same amount of fish (Kleisner et al., 2017). Adaptive management strategies will need to be employed, as range shifts will move fish stocks across management boundaries and established protected areas (Madin et al., 2012).

Circulation patterns in the Northwest Atlantic have undergone changes in recent decades, resulting in significant influences on regional ocean conditions. The Atlantic Meridional Overturning Circulation (AMOC) is one of the major circulation forces within the North Atlantic, and its strength is negatively correlated with the northerly position of the Gulf Stream (Zhang, 2008; Saba et al., 2016). When the Gulf Stream is in a more northward position, warm, deep water is transported closer to the continental shelf and results in increased temperatures in the Northwest Atlantic

(Zhang and Vallis, 2007). Ocean temperatures in the United States Northeast Continental Shelf have undergone large temperature increases where fall bottom temperatures over the past 45 years have increased by 2.1 °C for the Georges Banks and 0.8 °C for the Gulf of Maine. These temperatures are projected to reach 5.0 °C and 3.9 °C above current conditions respectively over an 80-year time period (Kleisner et al., 2017). Similar trends in circulation patterns have also affected the Scotian Shelf and Southern Newfoundland, where bottom temperatures since 2010 have reached 100-year record highs and are expected to remain elevated for the near future (DFO, 2017). Brickman et al. (2018) characterized this trend as part of normal fluctuations in the interactions between the Labrador Current and the Gulf Stream. Current conditions have resulted in a greater northern reach of the Gulf Stream, bringing warm water closer to the continental shelf. In the Gulf of St. Lawrence, this has caused inflows of warm, deep water into the Gulf via the Cabot Strait that was initially observed in 2010 (Galbraith et al., 2018). From the head of the Strait, these warm inflows take approximately four years to reach the head of the Laurential channel. Sustained by further warm inflows in 2012 and 2014-2016, maximum bottom temperatures throughout the GSL have increased by nearly 2 °C on average (Galbraith et al., 2018). Given that measureable distribution shifts in many fish species were detected in the North Sea (Perry et al., 2005) and the Northeast Continental Shelf (Nye et al., 2009) where temperatures have increased by approximately 1 °C, it is likely that marine taxa in Canadian waters are shifting in

response to warming conditions and efforts should be taken to monitor for such changes.

One such species noted to be expanding polewards is the silver hake (*Merluccius bilinearis*), a small gadoid species. Silver hake has historically been distributed along the Northwest Atlantic, with a southernmost extent along the Mid-Atlantic Bight and a northernmost extent on the Scotian Shelf. Since 2010, large quantities of silver hake have been encountered along the edges of the continental shelf in spring surveys of Southern Newfoundland (Rockwood, 2016), and they have recently been found in surveys of the Gulf of St. Lawrence where they have not typically been encountered (Bourdages et al., 2018). Silver hake is a demersally distributed species with a relatively narrow thermal optimum, typically being found at depths between 100 and 400 meters and at temperatures ranging from 5 – 10 °C (Scott, 1982; DFO, 2013), though it is known to travel to inshore waters during the summer to reproduce. Depending on the region in which it is found, silver hake attains a maximal length of approximately 45 – 60 cm and matures rapidly, with the majority of individuals attaining sexual maturity by age 2 (DFO, 2013; Alade and Traver, 2018). This species is known to be a voracious and opportunistic predator, and thus its diet is strongly dependant on prey availability and varies by region. In the Northeastern United States, from the Georges Bank and Gulf of Maine, their diets consist primarily of invertebrates in smaller individuals, with a marked shift to fish prey in individuals 25 cm and larger (Vinogradov, 1984). A significant cannibalistic effect is noted in these regions, a factor believed to influence the growth and

maturation of silver hake in the Northeast U.S. Meanwhile, a significant portion of Scotian Shelf hake's diet is comprised of euphausiids for both small and large individuals, and there is a smaller proportion of fish consumed as prey (Waldron, 1992; Cook and Bundy, 2010). Currently, it is not known whether silver hake is an important competitor or predator with existing Gulf species; elsewhere they have been suggested to act as a control on juveniles of other finfish species. Within the Georges Banks, silver hake is an important predator of the juvenile stages of forage fish such as herring and mackerel (Bowman, 1980; Tsou and Collie, 2001), although that influence may be diminishing in light of expanding spiny dogfish populations in response to regional warming (Tyrrell et al., 2008).

Silver hake's biology within the Gulf of St. Lawrence region has not been studied before, and the nearest study determined only their diet and distribution in Southern Newfoundland (Rockwood, 2016). An understanding of their biology and condition in this region can help reveal the potential impacts of this species. The purpose of my research was to generate knowledge on the biology of silver hake specifically within the Gulf of St. Lawrence, a geographic range edge where this species may be facing novel environmental conditions. Given the importance of quantifying range shifts and interspecific interactions in new environments and the potential impact of hake, my objectives were specifically to determine the diet, spatial distribution, and growth of silver hake within the Gulf of St. Lawrence, to investigate potential interactions with commercially important resident species, and to make comparison of hake's growth and condition with other regions. In chapter

two, I used stomach content analyses to determine hake's diet during the survey period, which could be compared with diets of other co-occurring species, and will discuss the potential impacts for both resident species and silver hake. In chapter three, I aged silver hake otoliths to determine growth rates compared length-weight relationships with nearby hake stocks to investigate the growth hake in the Gulf of St. Lawrence.

My research contributes to a greater understanding of the biology of silver hake in Gulf of St. Lawrence, as well as provides insights on interactions and limitations during the early stages of a range expansion. The data will provide a baseline description of both diet and growth for this new population. Finally, my interpretations can help inform fisheries management for both this species and those with which it may interact.

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1.2 Co-authorship Statement

I was co-supervised by Dr. Jonathan Fisher of the Fisheries and Marine Institute of Memorial University, and Dr. Dominique Robert of the Institut des sciences de la mer de Rimouski at the Université de Québec à Rimouski. I was responsible for the majority of the data collection required for this thesis, along with the majority of manuscript preparation and data analysis. In addition, chapter two, entitled "Silver hake's (*Merluccis bilinearis*) diet and spatial overlap with established competitors within its Gulf of St. Lawrence geographic range" was co-authored by Dr. Jonathan Fisher (Marine Institute), Dr. Dominique Robert (ISMER), and Dr. Denis Chabot (DFO). Dr. Jonathan Fisher and Dr. Dominique Robert helped conceptualize the study design, aided with statistical analyses, revised the manuscript, and provided financial support. Dr. Denis Chabot provided the redfish and Greenland halibut diet data used in the chapter and contributed to the interpretation of results. Chapter three, entitled "Individual growth rates and length-weight relationships of silver hake (*Merluccius bilinearis*) within the Gulf of St. Lawrence" was co-authored by Dr. Jonathan Fisher and Dr. Dominique Robert. Both contributed to the study design, assisted with statistical analyses, and made revisions to manuscript drafts for this chapter. I plan to submit both chapters to peer-reviewed journals following the formal submission of my thesis.

2. Silver hake's (*Merluccius bilinearis*) diet and spatial overlap with established competitors within its Gulf of St. Lawrence geographic range

2.1 Abstract

Increases in ocean temperatures are driving expansions of marine species' distributions into regions that have previously been unsuitable for their survival. These shifts may result in ecological consequences for native species such as altered predator-prey interactions. In the Northwest Atlantic, one example of a species undergoing distribution shifts is silver hake (*Merluccius bilinearis*), a small gadoid fish historically distributed from Georges Bank north to the Scotian Shelf. Following rapid warming of bottom waters in the Gulf of St. Lawrence since 2010, anomalous abundances of silver hake have been recorded by research vessel surveys in the Gulf, suggesting a northwards range expansion. Functionally, silver hake is of interest because it matures rapidly and is known to be an important predator of both invertebrates and fishes in other regions. Using silver hake samples caught during scientific surveys of the Gulf of St. Lawrence from 2015-2017, I quantified the trophic role of hake in this new region and compared it to diets in their historic range. I also studied the diet and spatial overlap between hake and two highly abundant, resident species (redfish, *Sebastes* sp., and Greenland halibut, *Reinhardtius hippoglossoides*). I found that silver hake preyed on abundant benthic invertebrates and fish species, which differs from findings elsewhere, which show more frequent predation of pelagic prey and cannibalism of juveniles. Diet and spatial overlap between hake and resident species were found to be high and are

hypothesized to contribute to the slow increase in hake abundance in the Gulf.

2.2 Introduction

Increases in ocean temperatures and changing circulation patterns have resulted in distribution shifts for many marine species worldwide (Perry et al., 2005; Zeidberg and Robison, 2007; Pinsky et al., 2013; Selden et al., 2017). In fact, relatively mobile marine taxa have been found to undergo shifts at rates that are upwards of an order of magnitude greater than rates observed in terrestrial systems (Sorte et al., 2010; Sunday et al., 2012). Under current warming regimes, the redistribution of marine species is likely to have consequences for the composition and productivity of marine ecosystems (Sorte et al., 2010; Doney et al., 2012; Hollowed et al., 2013; Hare et al., 2016). Asymmetrical responses by these species arise due to differential tolerances to abiotic environmental conditions, and such responses can alter ecosystem assemblages. This then leads to novel interspecific interactions and the intensification or weakening of pre-existing inter- and intra-specific interactions (Kempf et al., 2010; Hunsicker et al., 2013; Cormon et al., 2016). Shifting distributions can also have socioeconomic implications, as redistributions of biomass will affect the yields of fisheries that are slow to respond to such changes, while contributing to new opportunities within other areas (Pinsky and Fogarty, 2012; Hollowed et al., 2013).

In the Northwest Atlantic, enhanced warming patterns have already resulted in measured distribution shifts in several fish species, where regional temperature

trajectories have been identified as key drivers (Lucey and Nye, 2010; Pinksy et al., 2013). Ocean temperatures in the Northwest Atlantic are warming at 2 – 3 times the global average rate and bottom temperatures in regions such as the Northeast U.S. Shelf have increased by 0.8 – 2.1 °C over the past 45 years, driven by a weakening of the Atlantic Meridional Overturning Circulation (AMOC) in addition to enhanced regional forcing (Kleisner et al., 2017). In the Northeast U.S. Continental Shelf, a vulnerability assessment of fish and invertebrate species to climate change noted that approximately half of the 82 species assessed are likely to experience negative effects relating to productivity and abundance, and a majority are expected to undergo distribution shifts with rates varying by species (Hare et al., 2016). Similar to terrestrial examples, such asymmetrical responses by marine species are expected to affect interspecific interactions, with the potential for significant ecosystem impacts. For example, it has been hypothesized that the further retreat of Atlantic cod's distribution on the Northeast U.S. Shelf with increased ocean temperatures will reduce its spatial overlap with prey species such as herring and mackerel, and thus reduce its top-down influence within the ecosystem (Selden et al., 2017).

A similar warming trend has also been observed throughout Atlantic Canada, with the Scotian Shelf, Southern Newfoundland, and Gulf of St. Lawrence all experiencing anomalously warm bottom conditions (DFO, 2017a). Species here are likely to experience similar responses and impacts to those described in the Northeast U.S. Shelf region (Stortini et al., 2016).

Silver hake (*Merluccius bilinearis*) is an example of species undertaking pronounced geographic shifts under warming conditions in the Northwest Atlantic. In the Northeast U.S. shelf, the general trend has been a decrease in hake biomass in their southern extent on the Georges Bank and an increase in northern biomass within the Gulf of Maine (Nye et al., 2009; 2011). Nye et al. (2009) suggested that this trend is a function of shelf warming driven by changes in circulation, and ruled out the influences of fishing pressure and changes in productivity. Similar trends in hake distribution have been noted in Atlantic Canada with a rapid increase in silver hake biomass being recorded in Southern Newfoundland (NAFO division 3Ps), where since 2010, it surpassed Atlantic cod as the dominant piscivore by biomass (DFO, 2017b). This trend is also associated with some of the highest hake biomass estimates on the Scotian Shelf since the 1990s (DFO, 2018a). Further north, the emergence of hake in the Gulf of St. Lawrence (NAFO divisions 4RST) in 2013 and its persistence since then represents an anomalous condition, as prior warm periods had led to only scattered occurrences of this species in the Gulf (McKenzie and Scott, 1956). Both the Southern Newfoundland and Gulf trends represent a northward shift in abundance for a species that, in its Canadian range, has historically been concentrated on the Scotian Shelf (Helser et al., 1995; Mahon et al., 1998; Rockwood, 2016). Silver hake is known to be a voracious and opportunistic predator of both invertebrate and finfish species, and has been suggested to act as a control on other fish species such as haddock and mackerel through the predation of juvenile stages (Bowman, 1980; Helser et al., 1995). As such, the recent emergence of hake in the

Gulf regions raises questions regarding their impacts and interactions within this ecosystem.

Here I characterize several aspects of silver hake's biology in the Gulf, namely diet and environmental distribution that contribute to the knowledge of this species' dynamics in Atlantic Canada. Given that silver hake is known to be a voracious and opportunistic predator in the Northeast U.S. Shelf with the potential to affect stocks of other fish species (Bowman, 1980), diet information for hake within the Gulf can help determine its potential influence in this region with respect to its predatory pressure. This research also quantifies silver hake's diet at the northernmost extent of its distribution for the first time and establishes a baseline for future comparisons within and among ecosystems. Stomach content analysis was used to produce a detailed snapshot of this species' feeding habits in the late summer and was compared among different parts of its distribution. Furthermore, I aimed to investigate the spatial and diet overlap between the emerging silver hake and two commercially important and highly abundant resident species of the Gulf of St. Lawrence, the deepwater redfish/Acadian redfish complex (*Sebastes mentella*/*Sebastes fasciatus*) and Greenland halibut (*Reinhardtius hippoglossoides*). The two species are established predators, which are anticipated to share similar trophic roles with silver hake due to their demersal distribution in Gulf of St. Lawrence. Spatial and diet overlap were determined for the three species using survey and diet data from annual fishery-independent surveys. My research also builds on literature that characterizes the biology of aquatic, and especially marine

organisms that have undergone range expansions and their impacts in new geographic ranges. Finally, this research serves to inform those who are interested in both the potential for silver hake as a harvestable resource, as well as its impacts on established fisheries within the Gulf of St. Lawrence.

2.3 Methods

2.3.1 Study Region

The study area encompasses the Gulf of St. Lawrence, a large, semi-enclosed sea in Atlantic Canada that primarily receives inflow from the St. Lawrence River and has two outlets: the Cabot Strait to southeast, and the Strait of Belle-Isle to the northeast (**Fig. 2.1A**). The two straits also typically contribute minor surface inflows to the Gulf. Bottom conditions in the Gulf are dictated by the deep inflow of water that enters through the Cabot Strait and travels through deep channels to the St. Lawrence Estuary over the course of 3 – 4 years. A distinctive feature of the Gulf is the presence of the Cold Intermediary Layer (CIL), a cold stratified layer ($T < 1$ °C) which persists year-round in the Gulf. This layer occupies depths of around 40 – 120 m, becoming thinner during the late summer as surface waters warm and is regenerated in winter by cold freshwater inputs (Gilbert and Pettigrew, 1997; Galbraith et al., 2018).

For the purposes of scientific assessment and stock management, the Gulf is divided into the northern Gulf (NAFO divisions 4R and 4S) and the southern Gulf (NAFO division 4T). The Northern and Southern Gulf regions have distinct

bathymetries and thus experience different ranges of environmental conditions. The bathymetry of the Northern Gulf comprises many deep channels including the Laurentian, Anticosti, and Esquiman Channels, and has a maximum depth of ~550m (**Fig. 2.1A**). Bottom waters in these channels are relatively warm and high in salinity, and remain so year-round with little influence from the surface layer (Galbraith et al., 2018). Meanwhile, the Southern Gulf is relatively shallow throughout; generally <60 m deep with a maximum depth of ~130m. As the depth range of the CIL is typically around 20 – 120m, large portions of the shallow Southern Gulf bottom substrate is in contact with the CIL and experiences temperatures below 1 °C (Gilbert and Pettigrew, 1997).

Since 2010, the Gulf of St. Lawrence has been experiencing a warming trend in its bottom temperatures. Inflows of warm, deep water through the Cabot Strait and local forcing have resulted in an increase in average bottom temperatures by around 1°C, with warm conditions expected to persist for several years (Galbraith et al., 2018; Brickman and Wang, 2018). These warm conditions may also be driving increasingly hypoxic conditions in the deep channels of the Gulf. While conditions have been at a steady hypoxic level since 1984, dissolved oxygen concentrations have further declined since 2014 (Galbraith et al., 2018).

The ecology of the Gulf has also undergone several shifts in recent decades. Prior to the decline of the groundfish stocks in the 1970s and 1980s, Atlantic cod and other groundfish were the dominant species in the Gulf (DFO, 2018b). In the decades following the 1993/1994 temporary moratoria on Atlantic cod fisheries in

the Gulf (FRCC 2011), cod continued to decline while Greenland halibut and invertebrate species such as snow crab and northern shrimp became more abundant. With the recent warming of the Gulf, the trend has partly reversed and invertebrate abundances are decreasing, while species such as silver hake are expanding their northernmost range into the Gulf. At the same time, Atlantic redfish abundances are very high following several strong year classes (Bourdages et al. 2018).

2.3.2 Sample Collection

Samples of silver hake, redfish, and Greenland halibut were collected during two long-term, annual multi-species trawl surveys of the Gulf of St. Lawrence conducted by Fisheries and Oceans Canada (DFO) aboard the *CCGS Teleost*. The Northern Gulf survey is conducted during August of each year and encompasses NAFO divisions 4RS and the northern half of 4T while the Southern Gulf survey, conducted during September of each year, covers the southern half of NAFO division 4T. The Northern Gulf surveys follows standard procedures as outlined in Bourdages et al. (2018), where a Campelen 1800 shrimp trawl was employed and tows were 15 minutes long. Meanwhile the Southern Gulf survey used a Western IIA trawl and 30 minute tow times, and more detailed procedures are available in Savoie et al. (2016). Stratified random sampling strategies were used for both surveys, ensuring that the whole range of depths and bottom substrate within the Gulf was sampled. Data recorded from each set included individual lengths and

weights of fish species, latitudes and longitudes, depth, bottom temperature, dissolved oxygen, and salinity measurements. In this chapter, samples of silver hake, redfish, and Greenland halibut from the 2015, 2016, and 2017 Northern and Southern Gulf surveys were analyzed. Combined totals of 361, 329, and 314 sets (190, 167, and 188 Northern Gulf and 171, 162, and 126 Southern Gulf sets) were completed during 2015, 2016, and 2017 surveys, respectively. Silver hake were retained for diet analyses and were shipped frozen and stored at the Centre for Fisheries Ecosystem Research (CFER), at the Fisheries and Marine Institute of Memorial University. Samples of redfish and Greenland halibut from the same surveys were processed at the Maurice Lamontagne Institute in Mont-Joli, Quebec.

Subsampling protocols were used during the three years when retaining silver hake, redfish, and Greenland halibut for stomach content analyses. In 2015 and 2016, silver hake were subsampled based size classes of small (≤ 15 cm length), medium (16 – 30 cm), and large (≥ 31 cm) individuals, where a maximum of two randomly selected fish in each size class were collected per set. No distinction was made for the sex of the samples. Due to lower than expected abundances of silver hake in 2015 and 2016, all silver hake were collected for sampling in 2017. Greenland halibut were subsampled in 2015 from even set numbers, where one fish of each sex was randomly selected for each 5 cm size class from 20 to 45 cm (max 10 fish/set). Subsequently in 2016 and 2017, the protocol was adjusted to subsample at random five fish less than 30 cm in length, and five greater than 30 cm with no distinction between sexes. The subsampling protocol for redfish in 2015 selected

samples from odd numbered sets, retaining five fish smaller than 10 cm in length, five fish greater than 40 cm, and five fish in each 5 cm size class between 10 and 40 cm. This was adjusted in 2016 and 2017 to subsample five fish smaller than 20 cm and five fish greater than 20 cm in length from each odd numbered set. For all subsampling, efforts were made to exclude fish that showed visible signs of stomach eversion or regurgitation.

2.3.3 Stomach Content Analysis

Frozen silver hake were thawed in the CFER laboratory for sampling and stomach content analysis. The number of silver hake sampled was 91, 48, and 137 in 2015, 2016, and 2017 respectively. Characteristics including length, weight, sex, gutted weight, and liver weight were recorded for each sample and stomachs were removed and temporarily stored in individual bags with unique identification tags. Stomachs were dissected following sampling protocols outlined in Cook and Bundy (2010), and all prey items found in the stomachs were identified to the lowest possible taxonomic level.

Redfish and Greenland halibut stomach content analyses were completed at the Maurice Lamontagne Institute and followed comparable methodology to Cook and Bundy (2010). The total number of stomachs sampled was 1003, 579, and 564 for redfish and 690, 378, and 386 for Greenland halibut in 2015, 2016, and 2017 respectively.

Diet composition, pooled across all three years, was grouped into 5 cm length classes from 10 – 45 cm for silver hake and redfish, and 10 cm length classes from 10 – 60 cm for Greenland halibut. The proportion of each prey grouping within a length class was reported as percentages of the total prey weight within that length class.

In order to determine whether the total number of silver hake stomachs sampled (n=90) exceeded the number required to characterize silver hake prey diversity in the region, a rarefaction curve based on 100 randomized runs of the silver hake diet data was generated using EstimateS software (version 9.1.0, Colwell, 2013) that follows equations 5 and 6 outlined in Colwell (2004).

2.3.4 Design Weighted Distribution Curves

Cumulative distribution curves based on depth and temperature frequency distributions were calculated using a design-weighted method to take into account the stratified survey design, based on methodology from Perry and Smith (1994). Average biomass for each stratum was standardized against the number of trawlable units within that stratum; this is the stratum area divided by the average trawl area, which is a function of gear dimensions and tow duration. The average trawl area was standardized between the northern and southern Gulf surveys to account for differences in gear and tow duration.

The standardized biomass for each stratum was used to calculate its proportion within the overall survey area using the following formula.

$$proportion\ of\ biomass = \frac{mean\ stratum\ biomass * \#\ of\ trawlable\ units\ in\ stratum}{\sum standardized\ strata\ biomass}$$

The proportions were plotted against the average temperature and depth of each stratum to generate separate cumulative temperature and depth distribution curves for silver hake, redfish, and Greenland halibut in the Gulf. The cumulative distributions of depths and temperatures covered by the surveyed strata were also presented alongside the distributions of the studied species. These distributions were used to identify generally whether silver hake occupied similar depth and temperature niches as redfish and Greenland halibut. The overall strata distribution was included to observe whether the species were distributed in specific depths and temperature within the Gulf.

2.3.5 Spatial Overlap Analysis

Silver hake, redfish, and Greenland halibut catch data during the 2015 to 2017 surveys were used to investigate the spatial distributions and overlaps of the three species. From the preliminary diet data, euphausiids and pandalid shrimp were identified as particularly important prey for all three species (>25% combined contribution in each length class). Euphausiids were important prey for smaller individuals of the three species and pandalid shrimp made up greater portions of diets in larger individuals. For the purposes of the spatial distribution analysis, silver hake of lengths 25 – 40 cm, redfish of lengths 20 – 35 cm, and Greenland halibut of lengths 10 – 40 cm were considered due to these size classes exhibiting the greatest

initial amount of diet similarity for euphausiids and Pandalid shrimp and therefore the greatest potential for competition. Spatial intersection and mapping was conducted in R (version 3.5.3; R Core Team, 2018). Presence-absence for the designated size classes of the three species were mapped to 0.1 degree by 0.1 degree cells within the GSL, with all years pooled together. A species was determined to be present in a cell if it was collected during a set that fell within that cell region. The proportions of overlap between each resident species and silver hake were calculated by dividing the number of cells containing both species by the total number of cells containing silver hake.

2.4 Results

2.4.1 Distribution of Silver Hake in the Gulf of St. Lawrence

Silver hake in the Gulf of St. Lawrence did not occur at random with respect to temperature and depth. Hake were generally located on the slopes of deep channels such as the Laurentian, Anticosti, and Esquiman at depths of ~100 – 400 m (**Fig. 2.1**). Bottom temperatures from sets in which hake were encountered ranged from 1.3 to 7 °C, although over 75% of the design-weighted silver hake biomass was found in the deeper strata (~150 – 400 m) where bottom temperatures were between 5 and 7 °C (**Fig. 2.2 A,B**). In the three study years, hake were found throughout the northern Gulf, from the Estuary region to the Cabot Strait (**Fig. 2.1B**). Within the northern Gulf, hake were found in 26.4% of all sets from the three years of surveys, while the total occurrence of hake in southern Gulf surveys was

4.6%. Overall, hake were encountered in 15.8, 11.0, and 21.3% of all sets in each of the three years respectively. Despite the wide distribution of sets in which silver hake were encountered, the number of individuals caught in each set was low; in all sets which contained hake, on average only two individuals were caught per set.

2.4.2 Diet of Silver Hake by Size Class

Of the 276 silver hake sampled across the three years, 90 stomachs containing at least one identifiable prey item were examined, amounting to 39, 15, and 36 stomachs in 2015, 2016 and 2017, respectively. Prey diversity was relatively low and in total 11 prey species were identified in silver hake stomachs – six invertebrates and five finfish taxa (**Table 2.1**). Detailed identification of many fish prey in silver hake stomachs was not possible due to the prey being at an advanced stage of digestion and the absence of prey otoliths. The greatest number of different prey types that was found in a single Gulf hake stomach was three, while 78% of stomachs contained only one prey type. Due to the small number of stomachs available after the exclusion of everted and empty stomachs, diet data from the three survey years were combined in all further analyses. Pooling the diet data across years allows us to create a generalized characterization of silver hake's diet and to compare them to the diets of redfish and Greenland halibut. The rarefaction curve generated from the pooled sample of 90 stomachs indicated that our sample size was sufficient to capture ~95% of prey taxa that silver hake likely consume in the GSL and is thus sufficient for a general diet characterization (**Appendix Fig. A1**).

Silver hake's diet in the GSL consisted of several dominant prey species, and the total mass of each prey grouping is established in **Table 2.2**. Euphausiids, shrimp, capelin, and sandlance were the prominent prey items by mass in 2015 and 2017, while the primary fish prey for hake in 2016 was white barracudina instead of capelin. Redfish were also part of hake's diet but were only found in samples collected during the 2015 survey (**Fig 2.3B**). Invertebrates, including euphausiids and shrimp, were important in all size classes up to 40 cm and especially so in smaller individuals (<20 cm and 25 – 29 cm size classes) where invertebrates made up >70% of their diet. Silver hake appear follow a general increase in piscivory with increasing size classes, although the small sample numbers within the lower and upper size classes means that the trend is less certain (**Fig. 2.3A**).

2.4.3 Diet and Spatial Overlap Between Silver Hake and Resident Species

The diet composition of redfish and Greenland halibut in the Gulf were found to be similar to that of silver hake, with major contributions from euphausiids and pandalid shrimp (**Fig. 2.4**). For redfish, invertebrate prey made up a large majority of their diet across all size categories, while contributions from fish prey were present in redfish greater than 20 cm in length. Of the identifiable invertebrate prey, euphausiids made up a large proportion of the smaller size categories, while pandalid shrimp featured heavily in the larger size categories. Meanwhile, Greenland halibut diets comprised of similar proportions of invertebrate and fish prey in smaller size classes (<40 cm), and included primarily fish prey in the larger size

classes (>40 cm). Capelin contributions are notable in smaller individuals, while the main invertebrate prey transitions from euphausiids (<20 cm size class) to pandalid shrimp (20 – 40 cm).

Design-weighted cumulative depth and temperature distributions for redfish and Greenland halibut were similar to those of silver hake, although a smaller proportion of both redfish and Greenland halibut were found in sets shallower than 200 m when compared to silver hake (**Fig. 2.2**). When their spatial distributions were mapped to 0.1 by 0.1 degree cells, redfish were found in ~86% of the cells in which silver hake were present while Greenland halibut was present in ~78% of silver hake cells. In 76% of cells containing silver hake, both redfish and Greenland halibut could be found (**Fig. 2.5**). A total of 115 cells within the Gulf contained silver hake, while there were 615 redfish and 530 Greenland halibut cells.

2.5 Discussion

The nature and spatio-temporal variability of silver hake's diet composition constitute key knowledge gaps that prevent us from understanding the drivers and impact of their rapid range expansion in the Gulf of St. Lawrence. During the 2015 – 2017 Gulf of St. Lawrence surveys, silver hake were encountered throughout the deep channels of the region, which have been occupied since 2010 (Bourdages et al., 2018). Gulf hake's diet consisted of a mix of invertebrates including northern shrimp and forage fish species such as capelin and sandlance. The overall diet composition of Gulf hake differs from what has been reported in the nearby Scotian Shelf and the

Northeastern United States, where diets include major contributions from pelagic prey such as mackerel, herring, and squid – likely a function of differing prey availability among regions (Vinogradov, 1984; Waldron, 1992, Cook and Bundy, 2010). In addition, silver hake's depth, thermal, and spatial distributions were found to strongly overlap with two established predators: redfish and Greenland halibut. Within specified size categories, diets of the two established predators are similar to that of silver hake, and our results suggest that due to overlap in space and tropic roles, hake may face competition from these much more abundant resident species.

Since 2010, scientific surveys of the Gulf of St. Lawrence have yielded observations of relatively large numbers of hake in the Gulf, which have become widely distributed throughout the deeper channels (Bourdages et al., 2018). Although the recent emergence of hake in the Gulf has been notable, they have also been captured by fishermen during a period of warm conditions in the mid 1950s that pre-dated standardized surveys (McKenzie and Scott, 1956). Design-weighted depth and temperature distributions of hake from the 2015 to 2017 surveys were similar to results reported in other regions, which indicate a preference for waters in the 6 – 10 °C range and depths of approximately 75 – 250m (Scott 1982; Lock and Packer 2004). More recent data from Southern Newfoundland (NAFO Division 3Ps) collected by Rockwood (2016) show that silver hake are also found in warm and deep shelf slopes in that region (mean depth: 343 m, mean temperature: 6.59 °C). Similarities in temperature distributions are not unexpected, as hake are known to be sensitive to thermal conditions (Murawski and Finn, 1988; Helser et al., 2012),

leading to strong relationships between ocean conditions and their regional movements (Nye et al., 2011). However, the depth distribution of hake in the Gulf tends to be deeper than that seen in the Northeast U.S. Shelf, which can be explained by the unique oceanography of the Gulf. Where hake in the Northeast U.S. Shelf seek shallow waters (inshore – 100 m) to spawn during the summer (Helser and Alade, 2012), the presence of the CIL in the Gulf leads to bottom temperatures at depths of 60 – 120 m that are near 0 °C (Galbraith et al., 2018), far below the thermal tolerance range for hake. In effect, this excludes hake from a large portion of the Gulf, and instead they appear to be concentrated below 100 m in the deep channels of the Gulf. Increases in the intensity of hypoxic conditions in the deeper (> 300m) portions of Gulf, associated with the influx of warm water, are expected to negatively affect demersally distributed species (Stortini et al., 2016). While hypoxia likely affects silver hake, it does not appear to exclude them from the Gulf altogether and thus was not examined further this chapter.

Attempts at explaining range expansions for marine species have focused primarily on climate change and the warming trends experienced in different parts of the world (Perry et al., 2005; Last et al., 2011; Simpson et al., 2011). However, the effects of density dependent dispersal from a core population is also a key factor in range expansions (Best et al., 2007). This may be true for silver hake, as they have been shown to be a fish species that exhibit a positive abundance-distribution relationship on the Scotian Shelf (Fisher and Frank, 2004). An addition, the abundance of hake in the Scotian Shelf (DFO, 2018) and Southern Newfoundland

regions (DFO, 2017b) have been high in recent years and may be a contributing factor to this recent emergence in the Gulf. Given the responsiveness of this species to thermal conditions and the potential for stock mixing among the three established Northwest Atlantic stocks (Helser et al., 2012), warming has likely granted access to the Gulf, while high abundances in adjacent areas are providing the propagule pressure.

Despite these recent dynamics, the long-term persistence of silver hake in the Gulf is uncertain as it is unclear how long the anomalously warm bottom temperatures may last (Galbraith et al., 2018). Brickman et al. (2018) characterized this recent warming trend in Atlantic Canada as common and consider such trends as natural variability. A weakening of the warm, deep current flowing through the Cabot Strait will likely reduce the availability of thermally suitable (>5 °C) habitat, and may result in the departure of hake.

Furthermore, whether silver hake is truly established as a resident depends on its presence in the Gulf throughout the year. While a complete survey of the GSL occur once per year, additional temperature measurements through the water column are taken in March and June of each year. Averaged deep-water measurements revealed the persistence of warm conditions year-round, up to 7 °C, in the deep channels of the Gulf (Galbraith et al., 2018). Given the sensitivity and responsiveness of hake to bottom conditions, these sustained temperatures may support the year-round residence of silver hake within the Gulf. Additionally, the presence of age 1 fish encountered during surveys also lends further support that

that reproduction may be occurring within the Gulf (Zhu et al., unpublished (Chapter 3)).

The diet of silver hake in the Gulf contained some similar prey species to diets from other regions, although several notable differences that exist may be due to prey availability. Hake is known to be an opportunistic predator, leading to varied and diverse diets throughout its range (Vinogradov, 1984; Waldron, 1992; Rockwood, 2016). For example, diets of hake caught during summer surveys of the Northeast U.S. Shelf and the Scotian Shelf contained 31 – 38 and 30 prey species respectively (Vinogradov, 1984; Waldron, 1992). However, hake in the Gulf preyed on a limited number of taxa, with just 11 prey items identified among 90 individuals. On the Georges Bank, the southernmost region of hake's distribution, diets were dominated by euphausiids, Atlantic mackerel, squid, and juvenile silver hake (Vinogradov, 1984). Meanwhile in the northern range of its historical distribution on the Scotian Shelf, the diet of small hake was more invertebrate-dominated, consisting primarily of euphausiids and supplemented by some juvenile silver hake, pelagic fish such as Atlantic herring, and squid in age 3+ hake (Clay et al., 1984; Waldron, 1992; Cook and Bundy, 2010).

In contrast to silver hake found in the Georges Bank and Scotian Shelf regions, the diet of hake within the Gulf did not include many pelagic species or juvenile hake. Although Atlantic mackerel (*Scomber scombrus*) are found within the Gulf of St. Lawrence, they are primarily located in shallow (<100 m) inshore waters of the southern Gulf during the summer months (DFO, 2017c). Unlike in U.S. waters,

where hake migrate from shelf slopes to shallow, warm water during the summer (Helser and Alade, 2012), the CIL likely confines silver hake to the deeper channels (>100 m) in the summer. I hypothesize that the CIL is separating silver hake from their shallow-water, pelagic prey. Instead of diets composed of a mixture pelagic and benthic prey as described elsewhere (Clay et al., 1984; Waldron, 1992; Cook and Bundy, 2010), this separation may explain the greater reliance on benthic prey species by Gulf hake.

There was no evidence of cannibalism in silver hake of the Gulf of St. Lawrence. Cannibalism is common in other regions, where juvenile hake comprised up to 30 – 40% of adult hake's diet by weight in the Northeast U.S. Shelf (Vinogradov, 1984) and 25% on the Scotian Shelf (Waldron, 1992). This cannibalistic nature of silver hake has been suggested to be a density-dependent trait, and is thought to account for the majority of age 0 and age 1 hake mortality (Tsou and Collie, 2001; Link et al., 2012). The absence of cannibalism in our samples may be a function of lower hake densities in the region relative to the Scotian Shelf and Northeast U.S. Shelf. Survey results are not directly comparable between regions because gear, tow times, and therefore the catchability of hake vary (Bourdages et al., 2018; NEFSC, 2013; Clark and Emberley, 2011). However, the much greater abundances of silver hake caught per set in the northern U.S. and Scotian Shelf illustrates the differences in silver hake densities between regions. Fall NEFSC surveys from 2014 – 2016 averaged 19.92 kg/tow of silver hake in the northern management area and 1.05 kg/tow in the southern management area (Alade and

Traver, 2018), and a majority of sets in the 2016 July Scotian Shelf survey encountered >10kg/tow (DFO, 2017d). Meanwhile, catches of silver hake in the northern Gulf surveys peaked at 0.6 kg/tow in 2013 and have been at lower levels since then (Bourdages et al., 2018). Given the low abundance of silver hake encountered during Gulf surveys (average of ~2 individuals caught per set), if cannibalism is a density-dependent behaviour, hake densities in the Gulf may be too low to result in cannibalism.

In addition to regional variability in diets, the main prey of silver hake has been shown to change with the progression of the seasons, believed to be driven by the presence of different prey taxa at different times of the year (Waldron, 1992, Reed et al., 2018). At present, diet data for silver hake in the Gulf covers only the late summer period and diet compositions for other seasons are unknown. Future research into the diet of silver hake in the Gulf of St. Lawrence would benefit from sampling in multiple seasons to both confirm the year-round presence of hake and to investigate any seasonal variability in diet. In addition, this would allow silver hake diets to be comparable with other studies which involved sampling during different seasons (i.e. spring diets from Rockwood (2016)).

One limitation of this study was the small number of intact stomachs containing prey, an issue arising from the relatively low abundance of hake in the Gulf during the sampling years. This was compounded by the high rates of stomach eversion in the samples, a characteristic that is common to the species (Waldron, 1992; Rockwood et al., 2016). Although the sample size (n = 90) was sufficiently

large to provide a general description of silver hake's diet in the Gulf of St. Lawrence, the low number of samples for small (<25 cm) and large (>40 cm) individuals precluded more in-depth analyses. The continued sampling and investigation of stomach contents for hake in the Gulf of St. Lawrence will be necessary to enhance the level of detail for hake diets.

One major concern of the emergences of marine species in new ecosystems is the introduction of new predation pressures on resident species, and the potential impacts on both prey populations as well as species which share a similar trophic role (Kempf et al., 2010; Doney et al., 2012; Sunday et al., 2012, Selden et al., 2017). Silver hake in particular are known to be a key predator of several fish species in the Northeast U.S. Shelf and the Scotian Shelf (e.g. herring, mackerel) (Bowman, 1980; Waldron, 1992; Tyrrell et al., 2008). A close relative of the silver hake, the European hake (*Merluccius merluccius*), has also been demonstrated to have undergone a biomass shift in the Northeast Atlantic, and is believed to influence the abundance of an established predator (Cormon et al., 2016). There, the northward expansion of European hake's range resulted in greater spatial overlap with the commercially important saithe (*Pollacius virens*). Cormon et al. (2014; 2016) modelled the spatial overlap of the two species, and hypothesized that competition for prey may have contributed to a decline in saithe abundances. In the instance of the Gulf of St. Lawrence, the diet composition of emerging silver hake was found to be similar to that of Greenland halibut and redfish, two key predators in the system. Invertebrates such as euphausiids and pandalid shrimp, and forage fish species such as capelin

were found to be important components of the diet for each of the three species. In addition to consuming similar prey, a high degree of spatial overlap between the three species was found throughout the Gulf for the 2015 – 2017 sampling years, with both redfish and Greenland halibut being encountered in 67% of cells where silver hake were present. Spatial and diet overlap are often employed to investigate competitive and predatory interactions for fish species (Kempf et al., 2010; Kordas et al., 2011; Selden et al., 2017). These results suggest that while silver hake may represent a new source of predation pressure for euphausiids and shrimp populations, they may also be competing with resident redfish and Greenland halibut.

In particular, the current abundance of redfish in the Gulf region is exceptionally high, owing to the recruitment of several strong year classes in 2011, 2012, and 2013. This represents biotic conditions that have not been typical in the Gulf at least since 1990 (Bourdages et al., 2018). Both silver hake and redfish are found in deep and warm channels of the Gulf and the two species experience a high degree of spatial overlap, likely playing a factor in the similarity in their diets. Some predation of redfish by silver hake was observed in southern Newfoundland (Rockwood, 2016) and redfish were found in Gulf hake stomachs from 2015. However, they were not present in Gulf hake stomachs in 2016 or 2017, and individuals of the strong 2011 redfish year class may have since grown to sizes that are too large to be preyed upon by silver hake (see Figure 23 in Bourdages et al., 2018). Instead, the main interaction between silver hake and redfish may instead be

competition for prey. As of 2018, the biomass of redfish in the Gulf remains exceptionally high and individuals from that population have reached lengths greater than 20 cm, (see Fig. 23 in Bourdages et al., 2018) where shrimp consumption becomes significant.

Biotic resistance, either through direct predation or competition interactions, is often proposed as a factor that may hinder the establishment of marine species in a newly expanded range (deRiviera et al., 2005; Kimbro et al., 2013; Papacostas et al., 2017). While interactions with established species is just one of the numerous mechanisms regulating the success of a range expansion (Chuang et al., 2016), it is possible that the emergence of hake in the Gulf has been tempered by competition interactions with a strong redfish population. This may be why there has been a slower expansion of hake abundance here relative to southern Newfoundland, where hake abundances have increased rapidly in the absence of notable diet overlap with other highly abundant established predators (Rockwood, 2016).

In comparison to the Cormon et al. (2016) study where European hake abundances were estimated at nearly a quarter of that of saithe, silver hake abundances (indexed by survey catch rates) in the Gulf are approximately one thousand times lower than redfish abundances (Bourdages et al., 2016). Ultimately, silver hake's trophic influence remains small at this early point its establishment in the Gulf, and it is difficult to predict the future trend and influences of hake.

In a broader scope, the interactions between a species undergoing distribution shifts and resident species are important when considering the

potential ecosystem impacts of the expanding species. Distribution shifts of predator species have, and are expected to influence both top-down and bottom-up pathways within ecosystems (Zeidberg and Robison, 2007; Cormon et al., 2016; Westerbom et al., 2018). Efforts have been directed towards predicting spatial overlap between key predators and prey species, generally from a multi-species perspective (Kempf et al., 2010; Kordas et al., 2011; Cormon et al., 2014; Selden et al., 2017). However, species that are expanding into a new range may also face restrictive conditions such as the unique oceanography of the Gulf, which can influence trophic interactions (Ciannelli and Bailey, 2005). This study contributes to the growing pool of research of marine range expansions, and the factors regulating such expansions. The study of silver hake's biology within the Gulf of St. Lawrence may also be of interest to those interested in the redfish and Greenland halibut fisheries of the Gulf, as it can inform about the interactions and influences of silver hake, particularly where a related species has been suggested to impact abundances of a commercially desirable species (Cormon et al., 2016).

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2.7 Tables and Figures

Table 2.1: List of prey items identified in silver hake stomachs from the Gulf of St. Lawrence.

	Scientific name	**Common name**
Invertebrates	*Mysidae*	
	Hyperiidae	
	Weyprechtia pinguis	
	Euphausiidae	Krill
	Pandalus borealis	Northern shrimp
	Pandalus montagui	Pink shrimp
Fish	*Mallotus villosus*	Capelin
	Ammodytes sp.	Sandlance
	Arctozenus rissoi	White barracudina
	Phycis sp.	Phycid hake
	Sebastes sp.	Redfish

Table 2.2: Total mass, in grams, and frequency of occurrence of each prey grouping found within silver hake stomachs in the Gulf of St. Lawrence.

Grouping	**Mass of prey (g)**	**Frequency of occurrence (%)**
Euphausiids	47.16	38.9
Unidentified invertebrate	0.57	14.1
Unidentified fish	41.37	13.3
Hyperiids	0.66	8.9
Pandalus borealis	25.12	7.8
Unidentified Pandalid	4.51	5.6
Mysids	0.17	5.6
Capelin	37.46	5.6
Pandalus montagui	6.47	3.3
Sandlance	21.58	2.2
White barracudina	10.76	2.2
Redfish	21.17	2.2
Phycid hake	8.21	1.1
Weyprechtia pinguis	0.06	1.1

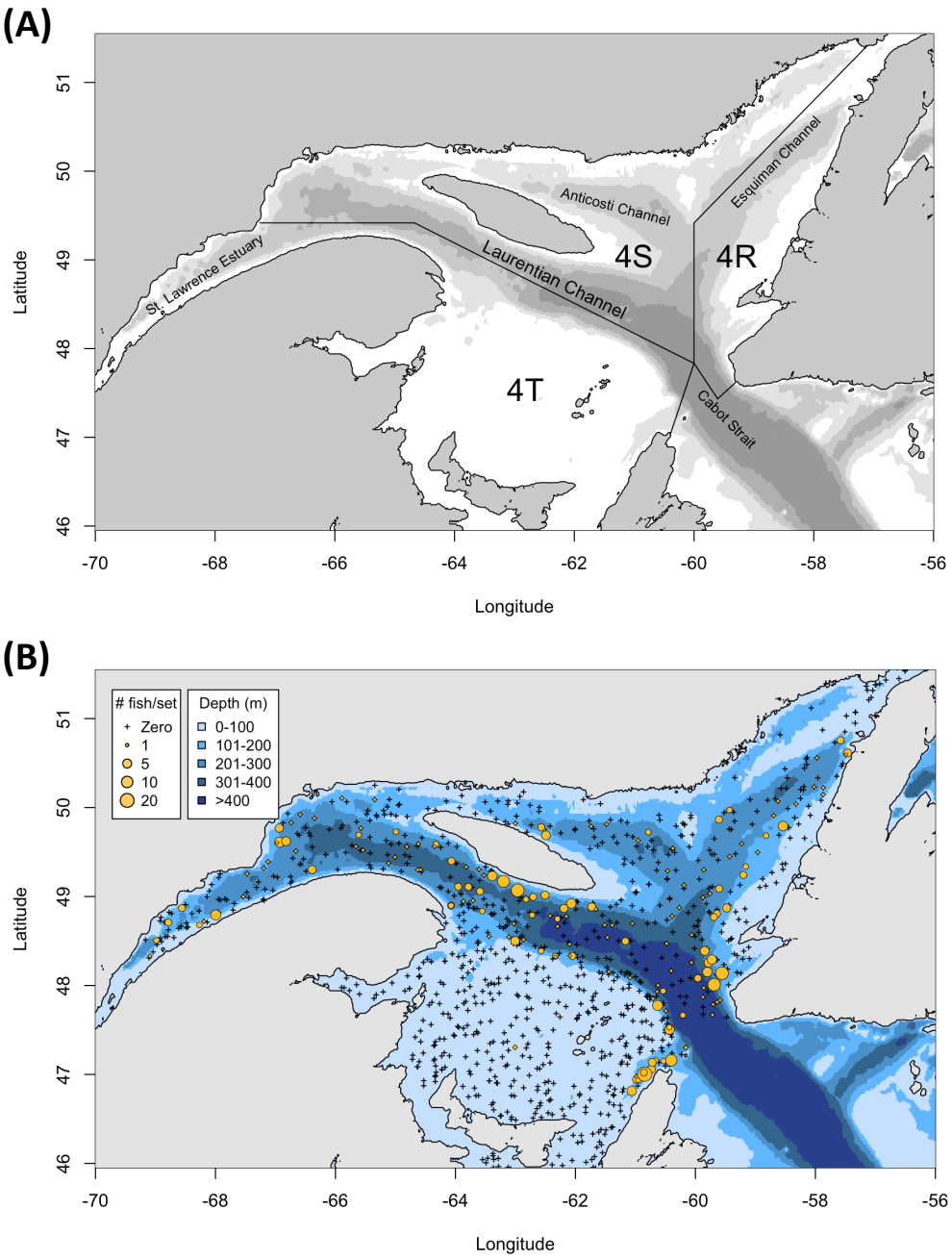

Figure 2.1: Maps of (A) NAFO divisions and locations of deep channels within the Gulf of St. Lawrence, and (B) set locations and the number of silver hake caught per sets during the 2015 – 2017 Northern and Southern Gulf surveys.

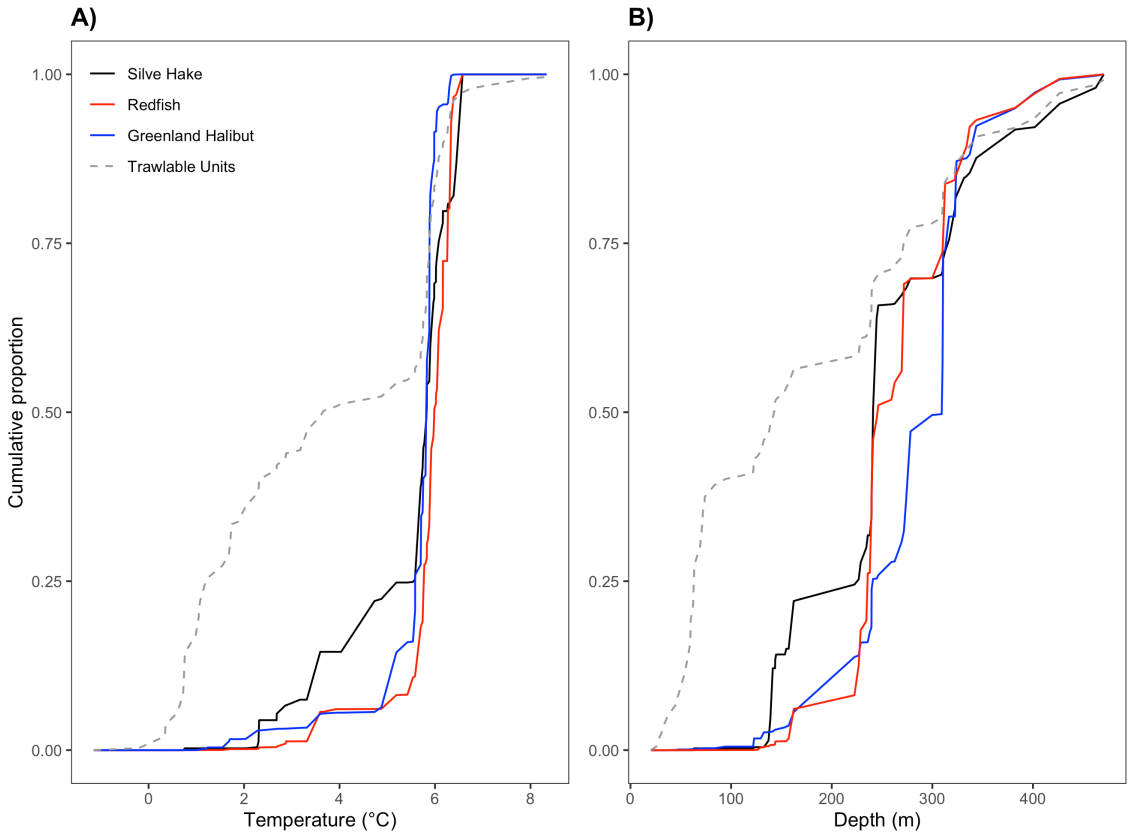

Figure 2.2: Design-weighted cumulative temperature (A) and depth (B) distributions of silver hake (black), redfish (red), and Greenland halibut (blue) caught during the 2015 – 2017 surveys of the Gulf of St. Lawrence. The grey dashed line denotes the cumulative distribution of the survey sets by strata area covered (trawlable units).

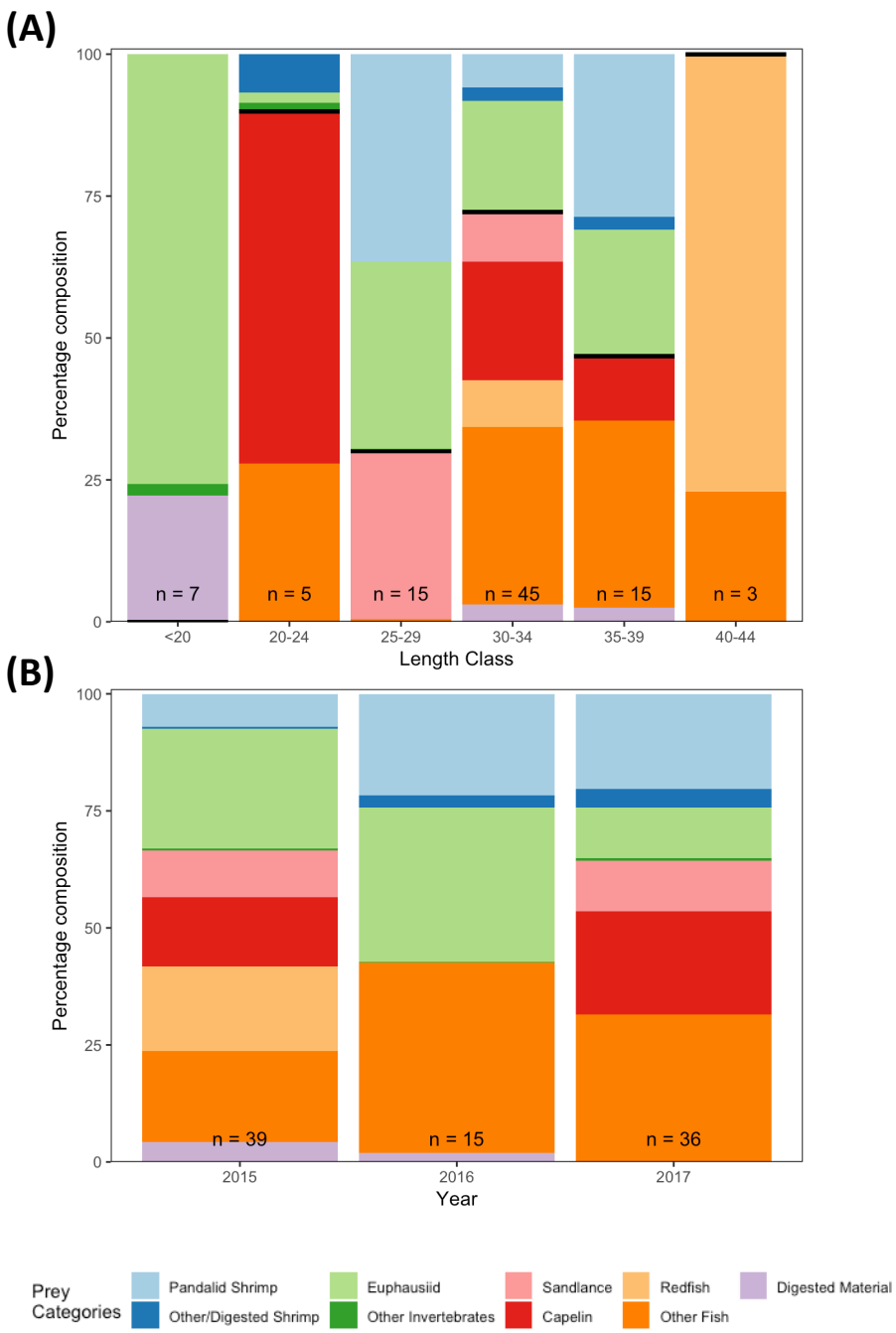

Figure 2.3: Silver hake diet composition as (A) percentage composition by weight of prey categories in different length classes and (B) in different survey years. The black lines in (A) denote the percentage of a length class' diet that is made up by fish prey.

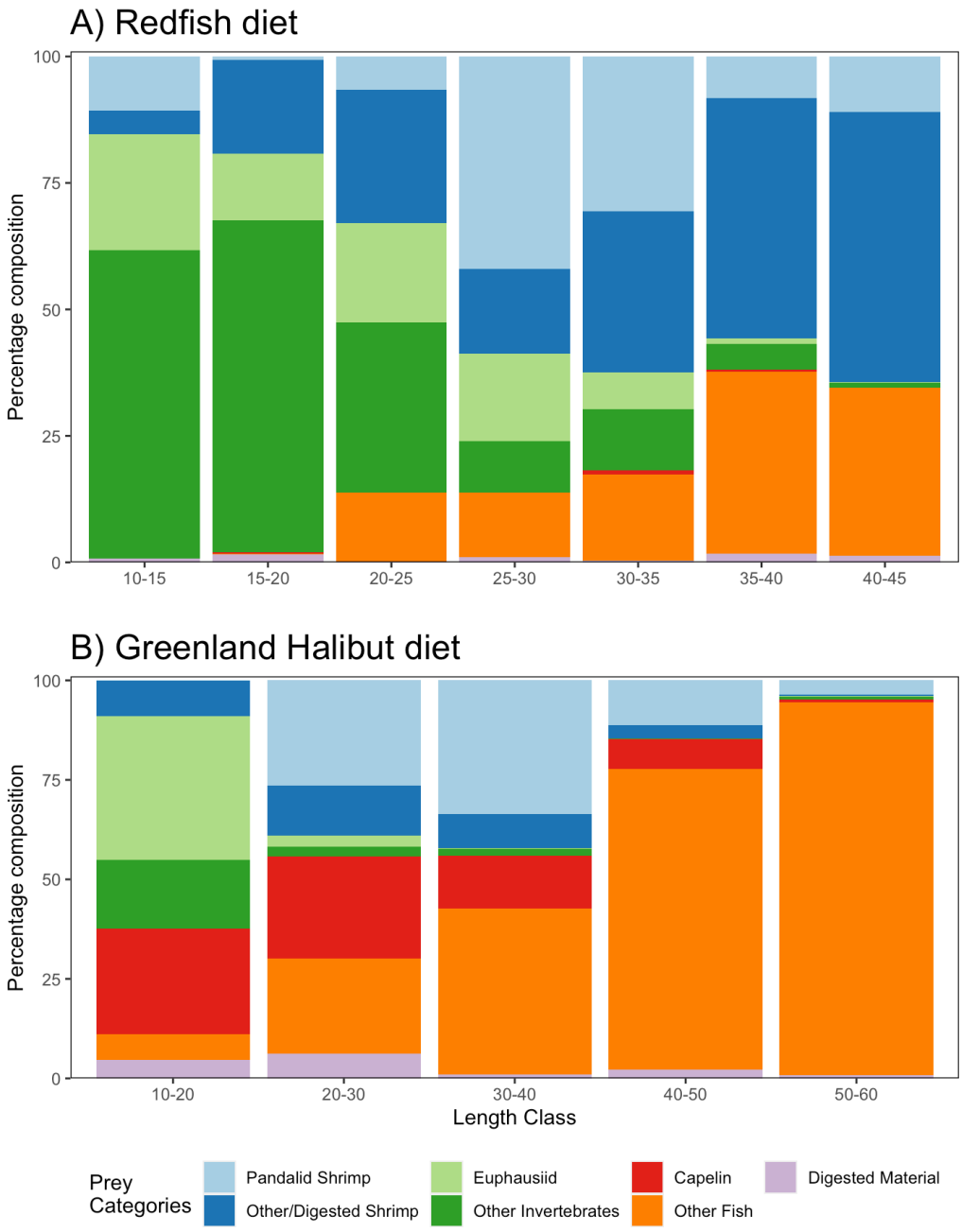

Figure 2.4: Percentage composition prey groupings by weight in the diets of different size classes of (A) redfish, and (B) Greenland halibut.

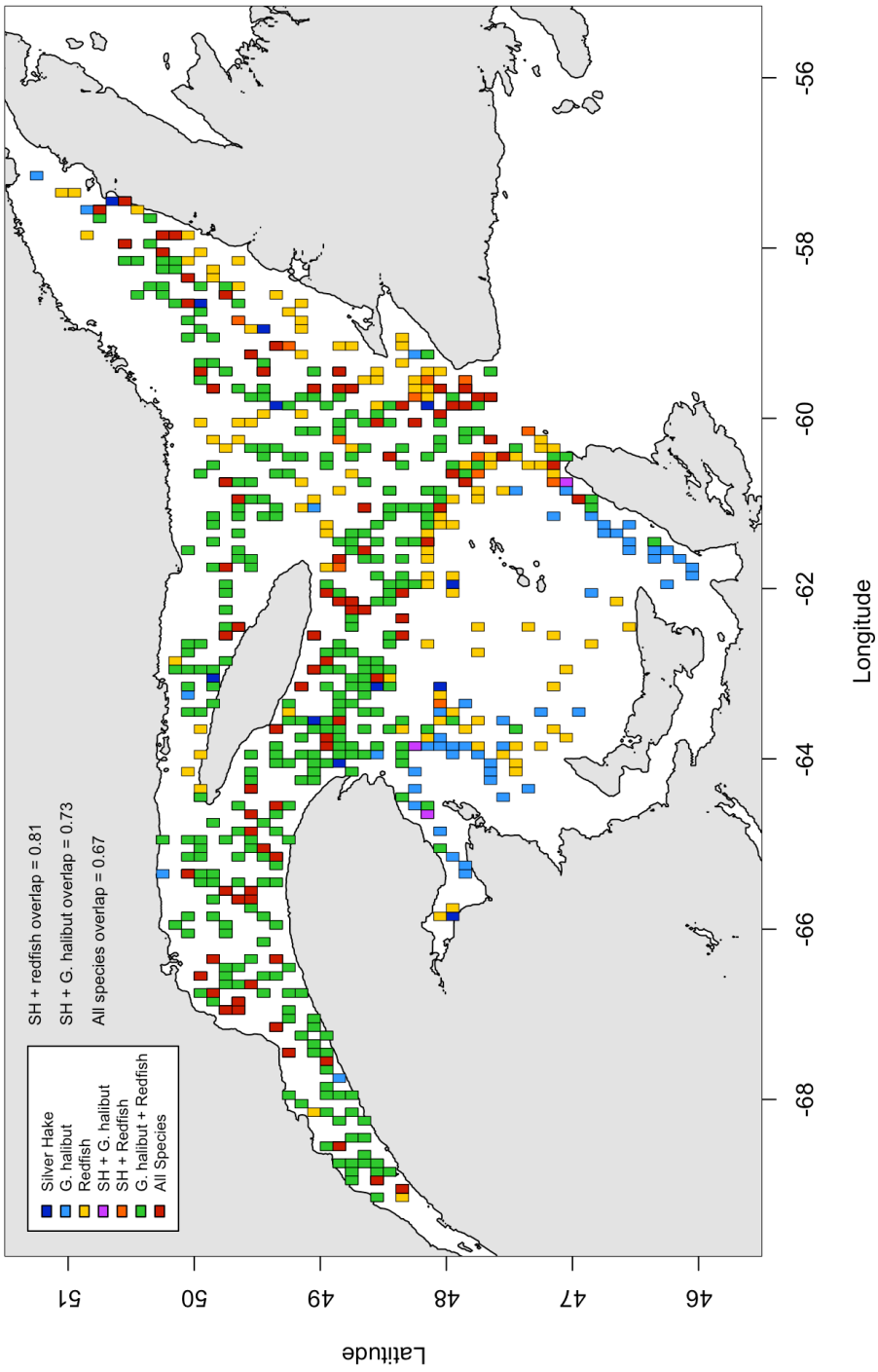

Figure 2.5: Map of silver hake, redfish, and Greenland halibut distributions and their overlaps based on data collected during the 2015 – 2017 survey periods. Sets containing silver hake of length class 25 – 40 cm, redfish length classes 20 – 35 cm, and Greenland halibut length classes 10 – 40 cm were included.

3. Individual growth rates and length-weight relationships of silver hake (*Merluccius bilinearis*) within the Gulf of St. Lawrence

3.1 Abstract

Regional warming results in distribution shifts of many marine species, forcing them into new habitats with variable environmental and biotic conditions. The position within the environmental gradient will likely impact individual condition and growth, with the possibility for either net positive or negative changes in the abundance of a given population. The recently-emerged silver hake (*Merluccius bilinearis*) within the Gulf of St. Lawrence constitutes a range edge population that is experiencing relatively cool temperatures, and is part of a different ecological assemblage relative to its core population on the adjacent Scotian Shelf. In the present study, I aged silver hake otoliths from the Gulf of St. Lawrence to determine their age structure and to fit von Bertalanffy growth functions to age-length data. Length-weight relationships were then compared between Gulf and Scotian Shelf hake to quantify potential differences in condition factor. Silver hake in the Gulf of St. Lawrence ranged from one to nine years of age, with a median age of four. Individual growth rates in the Gulf were found to be the highest among the regions of its range, while asymptotic lengths were the lowest. In addition, length-weight relationships revealed that Gulf hake had better body condition than Scotian Shelf hake. A release from strong density-dependent influences on growth may account for the greater growth rates, although it was not possible to identify specific drivers in this study. Growth and condition of hake at

this range edge reveal that these parameters are extremely plastic, which may be attributable to the combination of abiotic conditions and biotic differences in diet and competition.

3.2 Introduction

Warming ocean temperatures in many regions have resulted in shifts in the ranges of marine species towards the poles and to greater depths, a change that is associated with the availability of thermally suitable habitat (Perry et al., 2005; Last et al., 2011; Pinsky et al., 2013). Such shifts have been found to occur at rates up to an order of magnitude greater than those undertaken by terrestrial taxa (Sorte et al., 2010, Sunday et al., 2011). Because different species vary in their responsiveness to changing environmental conditions, asymmetric shifts in geographic range can result in the establishment of a small number of species in a newly expanded range. For example, smaller, quick-growing marine fishes with earlier ages at maturity were found to experience more rapid geographic shifts than long-lived species (Perry et al., 2005). The expansion of a species into a new region is similar to that of human-mediated biological invasions, as the establishment of a species under the two scenarios are regulated by similar factors (Hoffman and Courchamp, 2016; Sorte et al., 2010). Sorte et al. (2010) suggest that while the rates of expansion differ between the two scenarios, the ecosystem-wide impacts of range expansions can be as great as specific introductions.

Species that are introduced to new regions will face novel interactions that may determine whether they become abundant and widely distributed, or fail to establish within the new ecosystem. Both abiotic factors, such as ocean temperature, as well as biotic interactions (or lack thereof) are key factors that influence invasion success (Moyle and Light, 1996; Kimbro et al., 2013). For example, one theory often attributed to successful invasions is the enemy release hypothesis, which proposes that an invader's establishment in an area without natural predators enhances survival and proliferation of the invading species (Colautti et al., 2004; Prior et al., 2017). In addition, the characteristics of the invading species are also important, as those exhibiting opportunistic feeding patterns, quick growth and reproduction, and have wide environmental tolerances, are likely to become established and proliferate in the new ecosystem (Ricciardi and Rasmussen, 1998; MacMahon, 2002). Top consumers have also been hypothesized to often act as biotic multipliers of the effects of abiotic changes such as climate change (Urban et al., 2017). On the other hand, individuals in their expanded ranges may face novel environmental and biotic conditions that may limit their growth and proliferation. Biotic resistance can manifest through either direct predation on the expanding species by resident species or through competition for prey (deRivera et al., 2005; Chuang and Peterson, 2016).

Some examples of range expansions in aquatic systems have shown that biotic responses are dependent on species characteristics and ecological assemblages. For example, populations of non-native freshwater fishes at the edges

of expanding ranges were found to have higher condition factor and greater body size than those within the core population, likely owing to reduced intraspecific competition (Gutowsky and Fox, 2012; Lopez et al., 2012). Meanwhile, studies of marine invertebrates reveal variability in body sizes in newly invaded habitats, under influences from habitat-specific differences including high predation pressure and lower temperatures (Grosholz and Ruiz, 2003; Riley and Griffen, 2017).

The Northwest Atlantic is a marine system that has been warming rapidly in recent years, driven by several concurrent factors such as changes in Gulf Stream circulation and the effects of local forcing (Saba et al., 2016). The rate of warming on the Northeast U.S. Shelf is approximately double the global average rate, and the area has warmed by 0.8 – 2.1 °C over the past 45 years (Kleisner et al., 2017). Range shifts in numerous fish species of the Northeast U.S. Shelf have been recorded and many others are expected to be at risk of declining abundances with further warming (Nye et al., 2009; Hare et al., 2016). Parts of Atlantic Canada, including the Scotian Shelf and the Gulf of St. Lawrence, have also experienced intense regional warming, with both regions recording record high bottom temperatures since ~2010 (Galbraith et al., 2018, DFO, 2018a). Brickman et al. (2018) have determined this trend to be a result of variability in regional circulation patterns that is driving warm water onto the continental shelf. In particular, an inflow of warm, deep water penetrating into Gulf of St. Lawrence has raised maximum bottom temperatures by ~1 °C since 2010, and this trend is expected to persist in the mid-term (Galbraith et al., 2018).

The rapid warming trend in Canadian waters has created conditions with mixed impacts for resident species, while facilitating the growth and survival of species expanding their distributions from the south (Rockwood, 2016; Stortini et al., 2016). For example, silver hake (*Merluccius bilinearis*), a small gadoid species, has recently undergone an expansion of its northernmost range from its historical core population on the Scotian Shelf into the Gulf of St. Lawrence, where it has maintained a constant presence since 2010 (Bourdages et al., 2018). Although this is not the first record of silver hake in the Gulf that has been associated with warm periods, their presence in the past was scattered and short-lived (McKenzie and Scott, 1956). This recent trend appears to represent a more widespread and stable incursion into the region.

Silver hake is a demersally dwelling species that is distributed throughout the Northwest Atlantic, with historical concentrations (and managed stocks) on the Georges Bank, Gulf of Maine, and Scotian Shelf/Bay of Fundy. Previous literature has shown it to have a thermal tolerance of ~5 to 10 °C (Scott, 1982; Helser et al., 1995; DFO, 2018b), although hake within the Gulf was found in sets with bottom temperatures as low as 1.3 °C (Chapter 2). This species has also notably been shown to be responsive to changes in thermal conditions (Nye et al., 2011). Bottom water temperatures in deeper parts of the Gulf of St. Lawrence (>200m depth) have remained consistently around 5 – 7 °C year-round (Galbraith et al., 2018), and the region is hypothesized to support silver hake as a permanently resident species. However, the ecological role and biological parameters of this recently established

species in the Gulf are largely unknown, with most recent studies being conducted on the Scotian Shelf (Reed et al., 2018). In Chapter 2 of the present thesis, I studied the distribution and diet of hake, which is known to be an opportunistic predator (Bowman, 1980; Vinogradov, 1984), and here I investigate the growth and length-weight relationship for this species in its new range. Given that hake are believed to be limited in their growth and maturation rates by density-dependent effects (Helser and Almeida, 1997; Helser and Brodziak, 1998), its growth rates in the Gulf where densities are lower is a key ecological question. Growth rates and individual body size both influence rates of natural mortality, especially in early life stages where faster growth can reduce the potential of predation by other species and also allow individuals to consume a more diverse range of prey (Sogard, 1997; Gislason et al., 2010). I hypothesize that silver hake's growth in the Gulf of St. Lawrence will be slower than that which is reported in other regions, given the cooler bottom conditions and high abundances of resident species of the region as discussed in Chapter 2.

To determine growth characteristics within the Gulf, I aged individual silver hake using otolith thin sections. Hake's age distribution and their individual growth rates within the Gulf were used as one metric of this species' success here relative to other parts of its range. von Bertalanffy growth functions were used to generate growth parameters which could then be compared to results from other studies of hake populations along its geographic range. Hake's growth rates among different sections of its range (Scotian Shelf, Gulf of Maine, and Georges Bank) have been

shown to vary and are reported as age-length relationships (Hunt, 1978; Helser, 1996; Helser and Alade, 2012). Length-weight relationships were also employed to investigate potential differences in condition both between sampling years within the Gulf as well as between the Gulf samples and the nearby Scotian Shelf stock. Length-weight relationships have been used to characterize the type of growth experienced by fish species as well as to compare the condition and weight of different populations (Ma et al., 2017). These measures can be used to describe the "success" of a species at the edge of its newly expanded range. Finally, accurate and region-specific length-weight relationships are important inputs for both stock assessments and estimations of biomass, which can serve to inform stock management decisions (Rätz and Lloret, 2003; Gerritsen and McGrath, 2007).

3.3 Methods

3.3.1 Study Region

The Gulf of St. Lawrence is a large, semi-enclosed sea in Atlantic Canada that receives inflow from the St. Lawrence River, and has two outlets: the Cabot Strait to southeast, and the Strait of Belle-Isle to the northeast. Bottom conditions in the Gulf are dictated by deep inflows of water which enter through the Cabot Strait and travels through deep channels to the St. Lawrence Estuary over the course of 3 – 4 years. A distinctive feature of the Gulf is the presence of the Cold Intermediary Layer (CIL), a cold stratified layer ($T < 1$ °C) which persists year-round in the Gulf. This layer occupies depths of around 40 – 120 m in the Gulf, becoming thinner during the

late summer as surface waters warm and is regenerated in winter by cold freshwater inputs (Galbraith et al., 2018). This renders bottom temperatures of large parts of the Gulf, especially the shallow southern half, much cooler than that of deep channels. For fishery management purposes, the Gulf is divided into northern Gulf (NAFO divisions 4R and 4S) and the southern Gulf (NAFO division 4T) based partly on these characteristics (**Chapter 2, Fig. 2.1**).

Notably, the Gulf of St. Lawrence has experienced a warming trend in its bottom waters since 2010. Inflows of warm, deep water through the Cabot Strait and local forcing have resulted in an increase in average bottom temperatures of around 1°C, with warm conditions expected to persist for several years (Galbraith et al., 2018).

3.3.2 Sample Collection

Silver hake samples were collected from 2015 to 2017 during the fall multi-species depth-stratified trawl surveys of the northern and southern Gulf of St. Lawrence, conducted annually by Fisheries and Oceans Canada (DFO). The northern Gulf survey was completed in August of each year aboard the research vessel *CCGS Teleost*, and employ a Campelen 1800 shrimp trawl with 15 minute tow times (Bourdages et al. 2018). The southern multi-species survey occurred in September, following a different set of procedures, using a Western IIA trawl and 30 minute tow times (Savoie et al. 2016). A total of 361, 329, and 314 sets were completed in 2015, 2016, and 2017 respectively. These comprised 190, 167, and 188 sets in the

Northern Gulf and 171, 162, and 126 in the Southern Gulf. In 2015 and 2016, silver hake caught in each set were subsampled based size classes of small (≤ 15 cm length), medium (16 – 30 cm), and large (≥ 31 cm) individuals, where a maximum of two randomly selected fish in each size class were retained with no distinction between sexes. Due to the low abundances of silver hake in 2015 and 2016, subsampling procedures were changed such that all hake were retained for sampling in 2017. A total of 91, 48, and 137 silver hake samples were collected in 2015, 2016, and 2017 respectively.

3.3.3 Otolith Preparation and Sectioning

From all sub-sampled hake, the pair of sagittal otoliths were removed, dried, and stored in labelled envelopes. In preparation for mounting and sectioning, the left otolith from each pair was examined under a dissecting microscope to identify the location of the collum on the proximal surface of the otolith (**Fig. 3.1A**). When an otolith was broken in the core area or the core was otherwise unavailable, the alternate otolith of the pair was used instead. The location of the collum on the proximal surface corresponded to the location of the core within the otolith. A transverse line was drawn along the dorsal-ventral plane such that it intersected the collum, allowing for location of the core after embedding (**Fig. 3.1A**). Otoliths were placed in silicone trays containing twelve 25.4 mm by 12.7 mm by 5 mm moulds. A single marked otolith was placed in each mould with the proximal surface facing upwards, and was aligned such that the transverse line was parallel with the top and

bottom edges of the mould. Paper tags with the sample number were included for the identification of samples after embedding and sectioning.

A 5:2 mixture of Buehler EpoThin™ Epoxy Resin and Epoxy Hardener (30g resin to 12g hardener) was weighed and hand mixed for 2 minutes, then sonicated at room temperature for 5 minutes to remove small bubbles. The epoxy mixture was used to fill the 12 silicone moulds and toothpicks were used to remove large bubbles and to position the otoliths and paper tags. The epoxy was allowed to harden under a fume hood for ~24 hours before being removed from the moulds.

Epoxy blocks containing individual otoliths were sectioned into 0.4 mm sections along the pencil line with a Buehler IsoMet™ low-speed saw using a 0.4 mm spacer separating two 15LC saw blades. Sections were viewed in water with an Olympus S7X16 microscope at 2.5X magnification, and photographs of each side of the section were taken using an Olympus DP72 camera (**Fig. 3.1B**). Images were edited using Photoshop CS5 to enhance the contrast between opaque and translucent regions.

3.3.4 Otolith Ageing and von Bertalanffy Functions

Silver hake ageing training, advice, and use of silver hake otolith section reference collections were provided by the Fisheries Biology Program (FBP) Archives of the Northeast Fisheries Science Center (NEFSC) in Wood's Hole, Massachusetts, U.S.A. Archived reference collections that were previously aged by staff at the FBP formed a basis for training, and comprised of 254 samples collected

from scientific surveys and a further 254 samples collected from the commercial fishery. All reference samples were collected in 2015, the most recent year available. After ageing training, 262 reference samples randomly selected by strips (each strip containing 4 – 12 otoliths), were used to conduct two age agreement tests to ensure that ageing was carried out to the same standards as at the FBP.

Measurements of otolith increment widths were completed on images of the otolith sections, using the image analysis software, ImageJ (version 1.50i). The width of each otolith increment for each otolith was recorded. Most otolith sections could be measured, although 5 of the 224 samples appeared to be misshapen and could not be measured, possibly due to the angle of the cut or ontogenic effects during otolith development.

von Bertalanffy growth functions were generated separately for male and female silver hake, with samples from all years grouped for each sex. The ages and lengths of the immature fish, made up of age 1 individuals, were included in the functions for both males and females because sexually dimorphic growth and gonad development are not evident at these early ages. This analysis was completed in R (version 3.5.3) using the vbStarts function of the FSA package to determine starting parameters and the nls function in the stats package to fit the von Bertalanffy function (R Core Team, 2018, Ogel et al., 2020).

3.3.5 Length-Weight Relationships of Hake From Different Regions

Length-weight relationships for hake in the 2015-2017 sampling years were calculated for Gulf samples and the Scotian Shelf hake stock. Length and weight data for the Scotian Shelf silver hake stock were collected by DFO during their July Scotian Shelf multispecies trawl surveys (DFO 2018c).

Length-weight relationships in fish can be described using the following power-law relationship:

$$W = aL^b$$

Where W is an individual's wet weight in grams, L is its total length in cm, a is the condition factor, and b is the allometric growth coefficient. This relationship yields a linear relationship when log transformed, giving the following linear model:

$$ln(W) = ln(a) + b * ln(L)$$

Linear relationships were modelled with a region interaction term to determine if slopes (parameter b) were statistically different. If the interaction term was not significant at p = 0.05, the relationships were then compared using analysis of covariance (ANCOVA) to determine whether the intercept, or parameter ln(a) differed. Differences in the slopes and intercepts indicate differences in relative sizes and allometric growth. The same method was repeated with sampling year as an interaction term for Gulf samples. This analysis was completed in R (version 3.5.3; R Core Team, 2018).

3.4 Results

3.4.1 Precision Testing

Two sets of precision tests were completed with the reference otoliths loaned by the FBP. One test was conducted on 197 samples from the commercial fishery (% age agreement = 82.9%, Coefficient of Variance (CV) = 3.77%) and the second on 65 samples from the 2015 fall survey (% age agreement = 92.3%, CV = 1.42%) (**Appendix Fig. B1, B2**). Both of the precision test results met the FBP requirements for accurate ageing (CV < 5%, % age agreement > 80%)(NEFSC, 2017), ensuring confidence in the ageing of the Gulf silver hake otoliths.

3.4.2 Individual-Level Growth

The ages of hake subset from the Gulf samples ranged from one to nine years, with a median age of four for all years (**Table 3.1**). The von Bertalanffy functions showed that both male and female hake in the Gulf of St. Lawrence undergo the majority of their somatic growth in the first three years, reaching approximately 30 centimeters in length, after which growth slowed (**Fig. 3.2A, B**). The von Bertalanffy parameters from aggregated 2015-2017 ages and lengths for male silver hake were L_{inf} = 30.86 cm, k = 0.772 yr^{-1}, t_0 = 0.204, while parameters for female silver hake were L_{inf} = 35.46 cm, k = 0.703 yr^{-1}, t_0 = 0.229. L_{inf} and k parameters from other studies that summarize silver hake growth in the Scotian Shelf and Northeast U.S. Shelf (Hunt, 1977; Helser, 1996; Helser and Alade, 2012) can be found in **Table 3.2.** Simple comparisons of von Bertalanffy growth functions among different regions using these parameters are illustrated in **Figure 3.3**.

3.4.3 Length-Weight Relationships

The length-weight relationships generated from the linear models reveal that hake in both the Gulf of St. Lawrence and the Scotian Shelf show allometric growth coefficients which are greater than 3, indicating slight hyper-allometric growth (**Table 3.3**). When regions were used as a covariate, the interaction factor was significant ($p < 0.0001$), indicating that the slopes, *b*, differed between hake from the Gulf and Scotian Shelf. Gulf hake show a slightly steeper slope and have a larger allometric growth coefficient compared to Scotian Shelf hake (**Table 3.3**).

When sampling year was included as a covariate, we found that hake in the Gulf showed no statistical difference between slopes (parameter *b*) in each of the three years ($p = 0.85$) which range from 3.345 – 3.380 (**Table 3.3**). However, there was a significant difference between model intercepts ($p < 0.001$) and when recalculated as *a*, the 2015 model intercept (0.00238) was greater than the 2016 and 2017 values (0.00205 and 0.00203 respectively) (**Table 3.3**). Hake caught in 2015 had a greater *a* value, indicating a better condition factor at all lengths than those caught in 2016 and 2017.

3.4.4 Otolith Increment Analysis

Otolith growth trajectories for the year classes 2009 to 2014 were generated using the increment measurements (**Fig. 3.6**). First and second year increment widths, excluding the 2016 and 2017 year classes in which sample size were smaller than five individuals, remained relatively consistent in the 2009 – 2012 year classes.

Second increment widths in the 2013 and 2014 year-classes appeared to be greater and more variable than that of previous years (**Fig. 3.6**). Finally, growth trajectories varied among year classes, with the 2010 and 2011 year classes exhibiting the greatest mean length of the measured otolith cross-sections.

3.5 Discussion

Individual-level growth parameters and length-weight relationships within a fish population represent key information that can be used to evaluate its status and inform management. Investigating these characteristics for silver hake in the Gulf enhances our understanding of marine species responses at expanding geographic range edges. My results show that growth rates for silver hake in the Gulf of St. Lawrence are relatively high with much of their growth achieved by age three. The *k* values for silver hake in the Gulf were fairly similar to values from the nearby Scotian Shelf, while both male and female Gulf hake had smaller asymptotic values than the Scotian Shelf stock. Comparatively, asymptotic values for hake in U.S. regions (Gulf of Maine and Georges Bank) were much greater, although individuals in these populations grow at a slower rate. Hake with lengths that approach the Gulf of Maine asymptotic values (50-60 cm) are very rarely seen in the Scotian Shelf, and were not encountered at all in Gulf of St. Lawrence during the three years of surveys. In fact, the length distributions of hake in the two Canadian regions reach approximately 40 – 46 cm in their upper extremes (Bourdages et al., 2018; DFO, 2018b). Investigations of length-weight relationships showed statistically significant

differences in allometric growth coefficients between regions and differences in condition factor between sampling years in the Gulf, although the differences in parameter values are relatively small.

Both the age and length distributions for hake in the Gulf were relatively consistent between the three years of sampling. These results are similar to those from both the Scotian Shelf region (DFO, 2018b) and the Northeast U.S. Shelf (Alade and Traver, 2018), although the two other regions tend to have upper length ranges greater than that of the Gulf (presence of 40 - 55+ cm individuals). Interestingly, the median age of Gulf hake in all years was greater than that of the adjacent regions. This trend may be driven by an influx of migrants from the Scotian Shelf and Southern Newfoundland population, especially at a time when abundances are high in these adjacent regions (DFO, 2018b), and where silver hake are known to exhibit positive abundance-distribution relationships (Fisher and Frank, 2004). There is likely an age threshold for such migration as older individuals are more likely to have sufficient energy reserves to undertake such a migration. Other possible explanations could be poorer reproductive success or greater juvenile mortality in the face of lower ocean temperatures in the Gulf region, contributing to a reduced number of younger individuals. While this is speculative, as hake's reproduction in the Gulf was not studied, it was noted in chapter two that hake were limited to the deep channels of the Gulf during the late summer. This is in contrast to observations on the Scotian Shelf and Northeast U.S. Shelf where hake form spawning aggregations in shallower waters (<100m) throughout the summer months (Helser

and Alade, 2012; DFO, 2018c). The presence of the CIL in the Gulf may limit hake's access to the shallower portions of this region, potentially affecting their reproductive behaviour or the fate of their offspring. In addition, the generally lower water temperatures of the Gulf may also impact reproductive success, as the reproductive capabilities of marine fishes are influenced by environmental conditions (Yoneda and Wright, 2005). Future research would benefit from attempting to collect larval silver hake samples near known aggregations within the Gulf to confirm their presence, as well as investigating the origin of the silver hake within the Gulf using otolith microchemistry.

Individual growth rates and asymptotic lengths, as determined from von Bertalanffy growth functions, reveal more about silver hake's growth patterns in the Gulf. While the growth rate parameter *k* for both sexes of silver hake in the Gulf were the largest and asymptotic lengths (L_{inf}) were the lowest that have been reported in literature (Hunt, 1977; Helser, 1996; Helser and Alade, 2008), the differences between values from the Gulf and the nearby Scotian Shelf are minimal. The main differences exist between silver hake in Canadian stocks and hake of the US stocks.

Similarities between the Gulf and Scotian Shelf values are unsurprising, as the Gulf population likely comprises many migrants from the Scotian Shelf and ocean conditions are similar between the adjacent regions. Heavy fishing pressure on the Scotian Shelf since the 1970s led to a highly truncated age structure as many of the larger, older individuals were removed from the population, and currently a large majority of individuals are ages 1 – 2 (DFO, 2013). Such pressures have been found

to result in phenotypic shifts towards smaller individuals that are faster to reach maturity (Olsen et al., 2005), and could explain Gulf hake's short asymptotic length and high growth rate. Values from the Northeast U.S. Shelf as reported by Helser and Alade (2012), however, appear to differ from the Canadian regions with much slower growth rates and greater asymptotic lengths. While t_0 was not reported, the von Bertlanffy functions reported by Helser and Alade (2012) appear to have vertical intercepts from 20 – 25 cm, suggesting that those were lengths of age 0 individuals. I believed that these von Bertalanffy parameters were not appropriate for comparison with Gulf hake given the drastic differences. It is possible that a different fitting method was used in Helser and Alade's 2012 paper, which was not specified, leading to the differences in vertical intercepts. Instead, earlier values also reported by Helser (1996) for combined sexes were found to be more comparable and are presented in Table 3.2. These show that fish from the Northeast U.S. Shelf are generally larger, with slower growth rates. One caveat of this comparison is that the Scotian Shelf and Northeast U.S. Shelf values are older; otolith data were collected in 1976 and 1988-1992 respectively. It is possible that von Bertalanffy parameters have changed over time with changing population structures.

Length-weight relationships, a measure of the body condition of a population, were also assessed for hake from both the Gulf of St. Lawrence and Scotian Shelf. Parameters of this relationship can vary spatially and temporally for different populations. For example, differences in the availability of food, oceanographic conditions, and water quality have been implicated as factors that can influence this

metric (Ma et al., 2017). Inter-annual variability can arise from fluctuations in environmental and biotic conditions. This is especially true for silver hake in the Gulf, as both oceanographic and biotic conditions are undergoing a period of rapid change (Bourdages et al., 2018; Galbraith et al., 2018). A statistically significant difference in the condition factor of hake was noted between the three sampling years, although the differences are relatively small. In comparison to annual *a* values for Scotian Shelf from 1977 to 2011 (Stone et al., 2013), the values seen in the Gulf hake are quite similar to values observed since the mid 1990s and likely reflect interannual variability in prey and environmental conditions.

Differences in length-weight relationships are also likely to exist between a species' core range and its expanded range for species that are undergoing range expansions. Specifically, fish and invertebrate species have been found to have varying responses in body condition and length at leading range edges (Gutowski and Fox, 2012; deRiviera et al., 2015). The slope of the length-weight relationship for the Gulf differed significantly from those of the Scotian Shelf populations, indicating a difference in allometric growth. While this difference was statistically significant, examination of the allometric growth coefficients and the length-weight plots show that this difference is relatively small (0.07) and that the 95% confidence intervals are highly overlapping. The range of *b* within the same Northeastern US silver hake stock in different seasons (3.0606 – 3.1512) was similar in magnitude to the difference between Gulf and Scotian Shelf hake (Wigley et al., 2003). Although a

difference ultimately exists, it is not large enough to draw conclusions about biological differences between the Gulf and Scotian Shelf hake.

While the potential drivers of these differences in growth rates, asymptotic lengths, and length-weight relationships between the Gulf population and those of adjacent regions are numerous, here I present several hypotheses.

Several notable conditions, both oceanographic and biotic, have been characterized in the Gulf in recent years. The bottom temperatures encountered by hake in the deep channels of the Gulf range from 5 to 7 °C throughout the year (Galbraith et al., 2018). While these are exceptionally warm temperatures for the Gulf of St. Lawrence, they are at the lower range of silver hake's thermal optimum of 5 – 10 °C (Scott, 1982). In comparison, bottom temperatures in the southern half of the Scotian Shelf, where hake are concentrated, range from 6 – 10 °C year-round (DFO, 2018a; Hebert et al., 2018), while the Northeast U.S. shelf experiences temperatures from 7 to upwards of 16 °C (NEFSC, 2018). Temperatures near the lower end of a marine species' thermal tolerance results in slower somatic growth (Takasuka and Aoki, 2006; Neuheimer et al., 2011), and would be expected to influence silver hake's growth in the Gulf. While asymptotic lengths in the Gulf are the lowest in their range, growth rate is in fact the greatest. It is also possible that the lower bottom temperatures and potentially hypoxic conditions in the Gulf negatively influence older adults more than juveniles and younger adults, given that environmental preferences change between different life stages (Wigley et al., 2003).

In addition, silver hake are facing novel biotic conditions in the Gulf. The enemy-release hypothesis, commonly used in invasion biology (Colautti et al., 2004), suggests that species in a newly invaded region will face reduced predatory pressure if their main predators do not exist there. This is less strictly defined for marine fishes, as many species tend to be generalists and are highly mobile. Many of silver hake's known predators such as monkfish, Atlantic cod, and Atlantic halibut are present throughout the majority of its range (DFO, 2013), and it is unlikely that the Gulf presents a significant spatial refuge for hake.

Instead of reduced predator pressure as suggested by the enemy release hypothesis, hake are likely to encounter different levels of competition, both inter- and intraspecific. One of the unique biotic conditions currently found in the Gulf is the high abundance of redfish (*Sebastes sp.*), a species whose abundance in trawl surveys was three orders of magnitude higher than that of silver hake (Bourdages et al., 2018) and has been found to exhibit major spatial and dietary overlap with hake (Zhu, Chapter 2). In addition, Gulf hake have been demonstrated to have a relatively simple diet compared to other regions (Zhu, Chapter 2) and one of the major prey taxa for both hake and redfish, pandalid shrimp (*Pandalid borealis* and *P. montaguii*), has been found to be declining in the Gulf due to environmental factors (Bourdages et al., 2018). This interaction with the highly abundant redfish has the potential to negatively influence hake's growth though resource limitation. At the same time, silver hake are also known to exhibit density-dependent growth, where high densities on the Northeast U.S. Shelf has been suggested to negatively impact rates

of growth and maturity (Helser and Almeida, 1997). Compared to the Northeastern US where hake abundances are much higher (Alade and Traver, 2018; DFO, 2018b), densities in the Gulf are very low and individuals may benefit from reduced density influences. Although it was not possible to distinguish between the inter- and intraspecific pressures, it appears that the net effects are slightly faster growth rates, notably compared to those of the Northeastern US stocks. This agrees with several studies of freshwater species, which have found that individuals at range edges are characterized by greater growth rates, largely due to a release from intense intraspecific competition (Gutowski and Fox, 2012; Lopez et al., 2012).

Finally, I attempted to track inter-annual variability in growth using annuli measurements from the aged otolith sections. The measurement of distances from the core to annuli along fixed axes has been used in other fish species to back calculate growth and to generate chronologies (Neuheimer et al., 2011; Rountrey et al., 2014; Ong et al., 2015). Increment widths from all samples were averaged to produce growth trajectories for the 2009 – 2015 year classes. Where otolith growth is related to somatic growth in adult fishes, variability in the amount of otolith material laid down each year can indicate variation in growth rates, which can then be related to variability in environmental conditions. Some difficulty arises from attempting such a method in short-lived species; while chronologies based on otolith increments are commonly used in long-lived fish with well-defined annuli (Gillanders et al., 2012; Rountrey et al., 2014; Ong et al., 2015), shorter-lived species tend to have more poorly defined annuli. This was the case for silver hake, in

addition to the high variability in the widths of these increments. Here, I used the average length from the core to each annulus, for all individuals within a given year class. Nonetheless, I observed some variability in the otolith growth trajectories among silver hake year classes. Specifically, the 2010 and 2011 year classes appeared to have a more elevated trajectory when compared to the other year classes. This difference was more notable in third to fifth increment widths, which correspond to growth from 2012 onwards, during which bottom temperatures increased relatively quickly (Galbraith et al., 2018). However, the following year classes (2013 – 2015) had flatter growth trajectories. This trend may be related to the significantly smaller intercepts in length-weight relationships in the 2016 and 2017 silver hake, as both these trends indicate a condition in the Gulf that may be less conducive to silver hake's growth. However, the development of otoliths is generally understood to be influenced by a wide range of factors, and like hake's growth rates, it becomes difficult to identify a specific reason as to why later year classes did not show the same elevated trajectories.

One aspect not covered within my research is the origin of the silver hake that are currently found in the Gulf. It is unknown whether individuals found in the Gulf belong to a self-sustaining population, are migrants originating from adjacent regions, or are a mix of the two possibilities. This distinction will be key in defining silver hake as either a successfully established predator, or a species that is struggling and not yet established in this region. The older age structure of silver hake in the Gulf and the similarities in the von Bertalanffy parameters suggest that

these fish represent a steady migration of older individuals from nearby regions. Further research could use samples that have already been collected during my project and employ otolith microchemical methods and stable-isotope analysis to differentiate between established individuals and migrants, especially as the unique environmental conditions faced by hake in the Gulf could lead to unique microchemical signatures.

Results from the different analyses each highlighted the importance of environmental and biotic conditions in growth and condition of silver hake. While it is difficult to attribute my results to specific drivers, it is clear that Gulf hake are experiencing novel environmental and biotic conditions which contribute to differences in their growth characteristics and length-weight relationships when compared to stocks from other regions. Where silver hake exhibits many of the biological characteristics of successful invaders such as rapid growth and maturation rates, and a generalist diet, their future in the Gulf remains uncertain. These findings are also applicable to both assessment and industry purposes, as they serve to inform interested parties about the potential for silver hake as a harvestable resource. The von Bertalanffy parameters can be used to identify ages at which individuals become large enough to harvest, while length-weight relationships can be used in estimations of biomass. While hake abundances in the Gulf remain relatively low as of 2017 (Bourdages et al., 2018), this species has experienced major increases in its abundance in the southern Newfoundland region

(NAFO division 3Ps), demonstrating the potential for a similar trend in the Gulf of St. Lawrence.

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3.7 Tables and Figures

Table 3.1: Summary statistics for ages and lengths of silver hake in the Gulf of St. Lawrence

	Age (year)				Length (cm)			
	Min	**Max**	**Median**	**n**	**Min**	**Max**	**Median**	**n**
2015	1	9	4	71	12.1	45	31.2	156
2016	1	9	4	47	12.2	44	32.4	86
2017	1	8	4	90	10.2	45	31	158
Total	1	9	4	208	10.2	45	31.4	400

Table 3.2: Comparison of von Bertalanffy parameters in different regions of silver hake's distribution. L_{inf} is the horizontal asymptote of the function, k is the exponential coefficient, and t_0 is the x-intercept. The 95% confidence intervals are included in brackets for GSL parameters.

Region	L_{inf}	k	t_0	Years of data	Reference
Males					
GSL	30.86 (29.82, 32.24)	0.772 (0.574, 0.976)	0.204 (-0.109, 0.399)	2015-2017	-
SS	36.01	0.720	-0.078	1976	Hunt, 1977
GoM	56	0.15	N/A	1992-2008	Helser and Alade, 2008
GB	42	0.29	N/A	1992-2008	Helser and Alade, 2008
Females					
GSL	35.46 (34.56, 36.78)	0.703 (0.543, 0.901)	0.229 (-0.044, 0.440)	2015-2017	-
SS	37.88	0.638	-0.148	1976	Hunt, 1977
GoM	67	0.14	N/A	1992-2008	Helser and Alade, 2008
GB	55	0.21	N/A	1992-2008	Helser and Alade, 2008
Combined					
GoM	44.88	0.345	0.092	1988-1992	Helser, 1996
NGB	42.47	0.399	0.161	1988-1992	Helser, 1996
SGB	39.71	0.425	0.175	1988-1992	Helser, 1996
MA	41.25	0.472	0.471	1988-1992	Helser, 1996

GSL = Gulf of St. Lawrence, SS = Scotian Shelf, GoM = Gulf of Maine, GB = Georges Bank, NGB = Northern Georges Bank, SGB = Southern Georges Bank, MA = Mid-Atlantic

Table 3.3: Length-weight linear regression model parameters for Gulf samples collected in different years, and for pooled Gulf and Scotian Shelf samples from 2015-2017.

Between years in Gulf	ln(a)	a	b	SE (b)	r^2	n
2015	-6.0394	0.00238	3.34477	0.05117	0.965	156
2016	-6.1923	0.00205	3.37691	0.05533	0.978	86
2017	-6.2021	0.00203	3.38048	0.03878	0.980	158
p value	**<0.001**		**0.85**			
Between regions						
Gulf of St. Lawrence	-6.1865	0.00207	3.38037	0.02433	0.980	393
Scotian Shelf	-6.0310	0.00240	3.31544	0.00760	0.986	2545
p value	**<0.0001**		**<0.0001**			

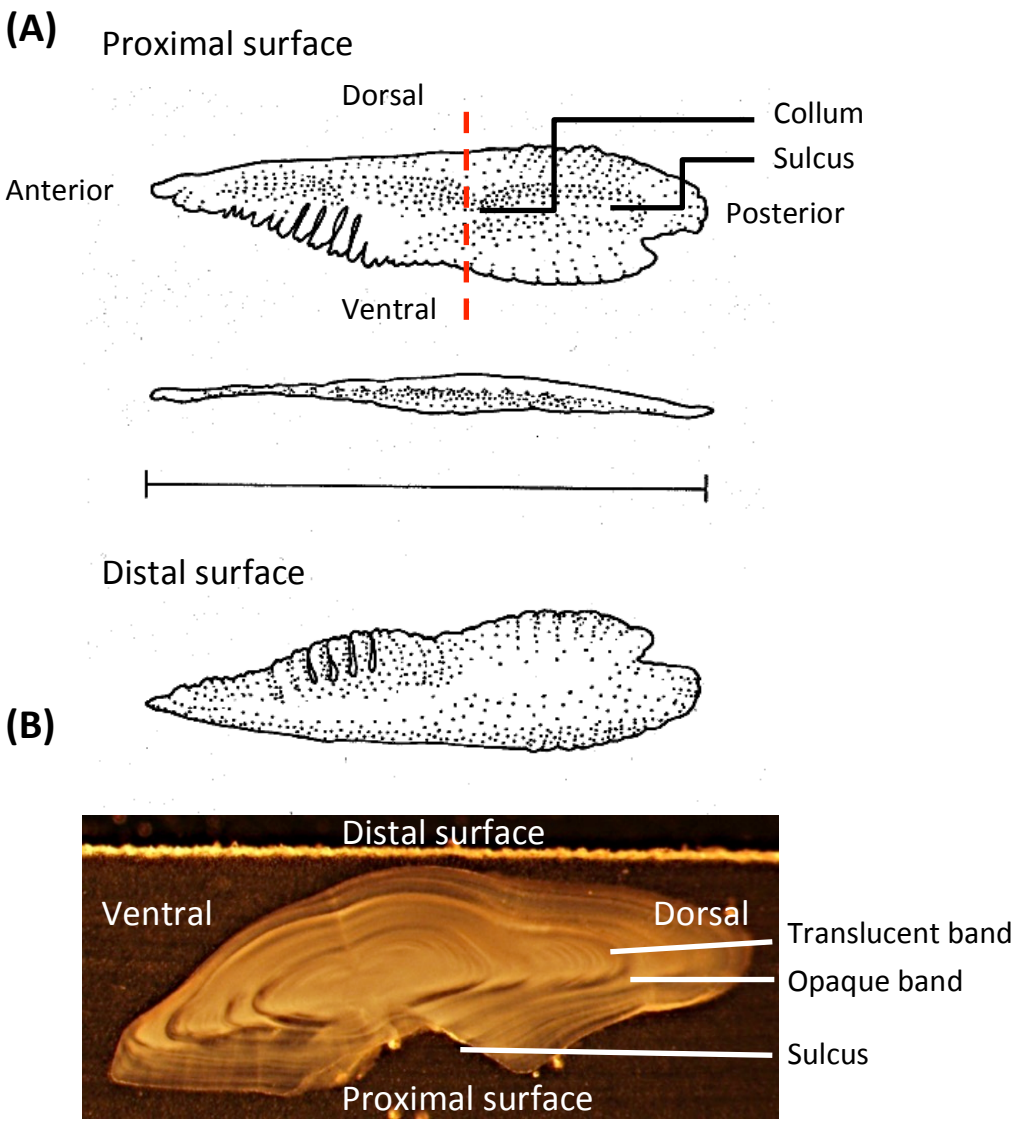

Figure 3.1: (A) Annotated silver hake otolith illustration, source from Brodeur's Otolith Guide (https://www.nefsc.noaa.gov/fbp/oto-guide/). The sulcus is the depression on the proximal surface of the otolith that runs along the anterior-posterior axis. The collum is the narrowing of the sulcus approximately midway between the anterior and posterior ends and indicates the otolith core. The dashed red line marks the pencil marking and the axis used for sectioning. (B) Annotated silver hake otolith section indicating the various surfaces and internal structures.

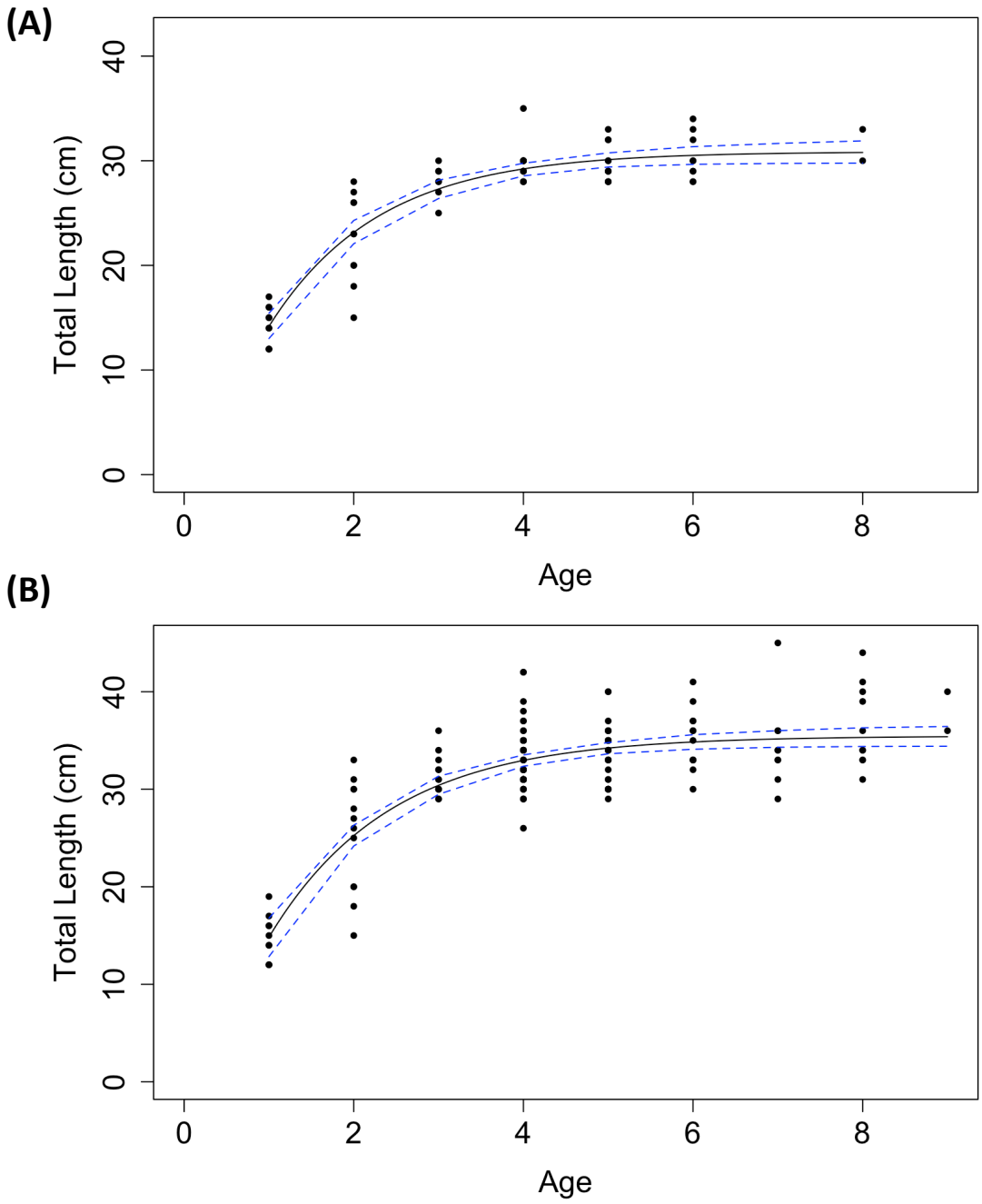

Figure 3.2: von Bertalanffy curve fitted to individual points for (A) male and (B) female silver hake within the Gulf of St. Lawrence. The blue dashed lines represent 95% confidence intervals calculated via the bootstrap method.

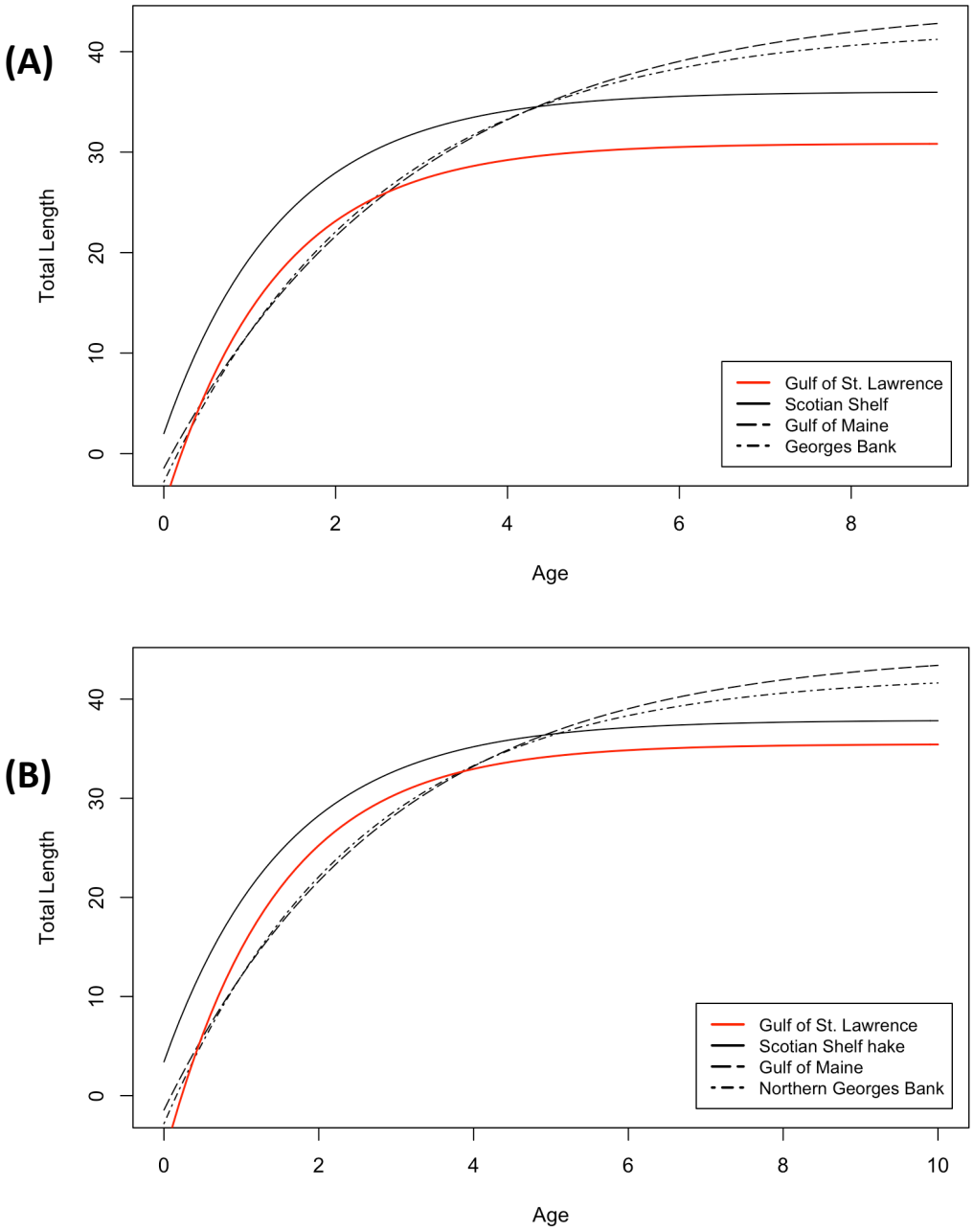

Figure 3.3: von Bertalanffy curves for (A) male and (B) female silver hake stocks from four different parts of its range.

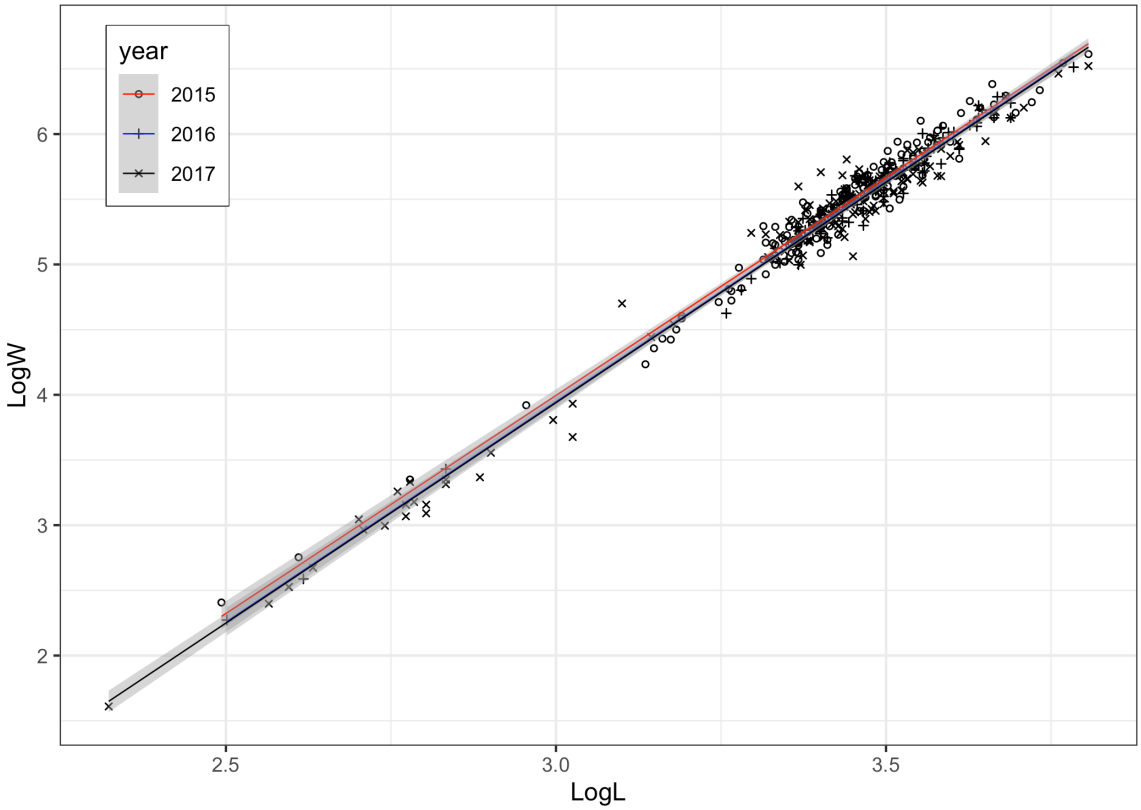

Figure 3.4: Linear regressions of log-transformed weights against log-transformed lengths for silver hake collected during the 2015-2017 Gulf of St. Lawrence surveys. Grey areas represent the 95% confidence intervals for the fitted regressions.

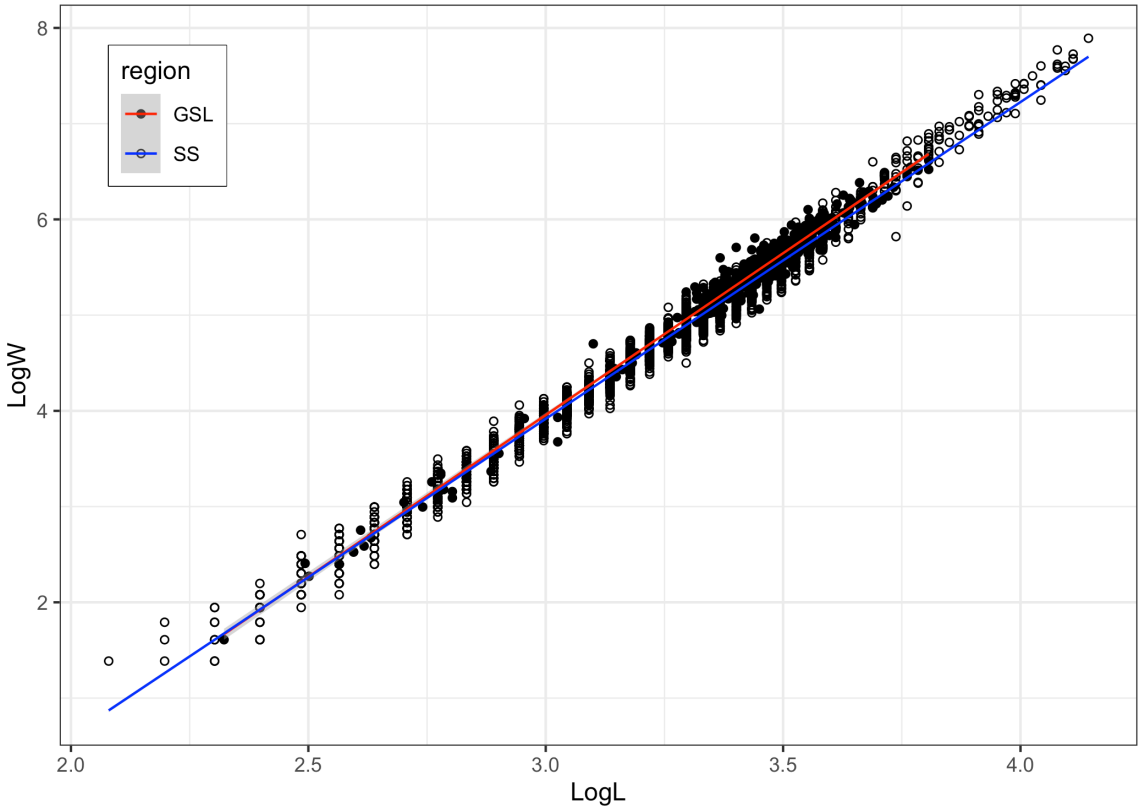

Figure 3.5: Linear regressions of log-transformed weights against log-transformed lengths for silver hake collected during the 2015-2017 Scotian Shelf and Gulf of St. Lawrence surveys. Grey areas represent the 95% confidence intervals for the fitted regressions.

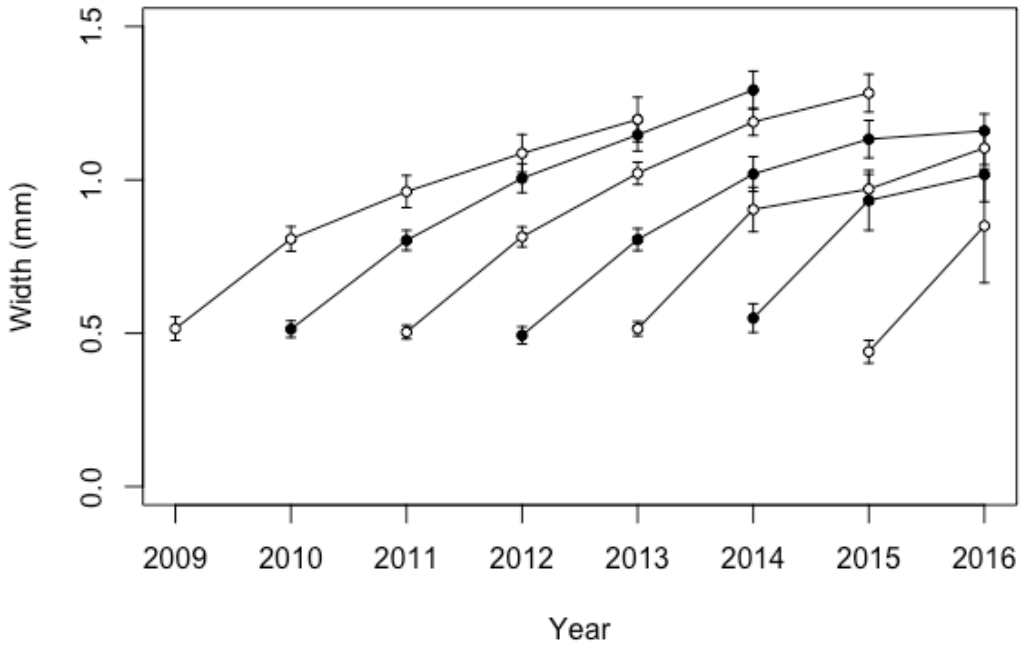

Figure 3.6: Growth trajectories of otolith widths for silver hake of the Gulf of St. Lawrence. Each trajectory represents a distinct year class, and error bars represent 95% confidence intervals. Filled and empty circles are used to distinguish between adjacent year classes.

4. General Discussion

The Gulf of St. Lawrence is an ecosystem that is undergoing rapid change in both environmental conditions and dynamics (Stortini et al., 2016; Galbraith et al., 2018). The recent emergence of silver hake in the Gulf of St. Lawrence is a significant trend that is likely driven by fluctuations in environmental conditions; however the ecological impact of this trend is unknown. Sorte et al. (2010) suggest that impacts from these range expansions could have effects on marine ecosystems at a magnitude similar to that of biological invasions. My research attempted to characterize silver hake's biology in the Gulf region such that it can provide some answers of their potential impacts here.

In my second chapter, I identified silver hake's main prey within the Gulf of St. Lawrence, which were composed primarily of demersal species such as shrimp, sandlance, and euphausiids. Characterizing the diet of a species is important; predation and competition interactions are some of the major avenues through which a species can influence an ecosystem. Diets in marine fishes are highly related to prey availability, which varies spatially and temporally, meaning that diet information gathered from different regions at different times are likely not interchangeable. For example, the two latest analyses of silver hake diets on the nearby Scotian Shelf from 2008 and 1986 (Waldron, 1992; Cook and Bundy, 2010) differ, where Cook and Bundy (2010) reported major contributions from Clupeids that were not observed in Waldron's (1992) report. Thus, my results provide recent and relevant diet information for hake in the Gulf region. I found that silver hake in

the Gulf preyed heavily on invertebrates such as euphausiids and pandalid shrimp, with some finfish contributions from capelin and sandlance. These results were similar to diets reported in southern Newfoundland (Rockwood, 2016) and the Scotian Shelf (Waldron, 1992), although no cannibalism was observed in Gulf hake.

I also identified high levels of co-occurrence and diet similarity between silver hake and two abundant resident species: redfish and Greenland halibut. Although predation and competition are significant influences on the mortality of fish stocks, they are not often considered when determining natural mortality (Kempf et al., 2010). Poorly defined natural mortality rates can lead to inaccuracies in the assessments of stock sizes. Understanding the influences of emergent species is therefore important in maintaining accurate estimates for the management of fisheries. This is especially true in the case of silver hake, which has been hypothesized to strongly influence herring and mackerel stocks on the Georges Bank through predation of juveniles (Bowman et al., 1980). While I found little direct predation by silver hake on resident redfish and Greenland halibut, their diets were similar and include major contributions from euphausiids, capelin, and sandlance. The current abundance and influence of hake in the Gulf are low, but there is the potential for rapid population growth in the future, similar to what has been observed in southern Newfoundland and resulting in interspecific competition for the resource (Rockwood, 2016). By understanding silver hake's interactions with resident species, we can enhance our understanding of their influence in the ecosystem.

At the same time, I hypothesized that environmental limitations posed by the Cold Intermediary Layer may be constraining the distribution and diet of silver hake in the Gulf. Where silver hake in other regions travel to inshore waters during the late summer, hake still inhabited the deep channels in the Gulf during the August survey (Helser and Alade, 2012). Influences of the local landscape often dictates predator and prey overlap. For example, inter-annual variability in cold-water masses in the Bering Sea influences the strength of the trophic linkage between cod and capelin (Ciannelli and Bailey, 2005). The conditions in the Gulf may impose a limit on the diet variability of silver hake and force them in competition with highly abundant resident species, which may have led to slower population expansion compared to that seen in southern Newfoundland (Rockwood, 2016). At the same time, declines in dissolved oxygen in deep channels of the Gulf are projected to reduce the density and distributions of resident species such as Greenland halibut (Stortini et al., 2016), and will likely affect silver hake as well. While my research did not focus on the influence of environmental conditions on silver hake, it is interesting to see the potential effects on diet and distribution of this species. Environmental conditions therefore constitute an important factor that may work to limit range expansions in other species.

Ages and growth rates are often characterized for distinct fish stocks and accurate catch-at-age results are a central component of fishery stock assessments (Lai et al., 1996; Campana, 2001). In my third chapter, I aged Gulf silver hake using otoliths and assessed their growth rates using von Bertalanffy growth functions. I

identified that silver hake in the Gulf grow rapidly, but attain relatively short maximal lengths compared to Northeast U.S. Shelf stocks. Such differences can be due to environmental conditions, notably temperature and dissolved oxygen in the Gulf, as well as competition for resources and even prey quality (Takasuka and Aoki, 2006; Neuheimer et al., 2011). In addition, resource requirements at different life stages differ for a species, and the availability of these different resources can vary between regions.

In addition, I also assessed length-weight relationships and compared these relationships between years within the Gulf and between the Gulf and Scotian Shelf. Silver hake in the Gulf were found to have a significantly greater allometric growth coefficient from that of the Scotian Shelf, although the magnitude of this difference was similar to variability that which is observed within a single stock over several years. My research is a first step in attempt to quantify silver hake's growth and condition in this new region, and further research can expand on this by investigating additional measures of individuals' conditions such as the hepatosomatic index and tissue composition. Larval survival and growth could also be assessed to investigate the reproduction of silver hake under the influence of the CIL, which could pose a barrier for reproduction in the Gulf.

Currently, age determination for silver hake in Atlantic Canada is not completed using otoliths, but rather the use of statistical methods based on the ageing of a small subset of hake otoliths (Campana and Fowler, 2012). While otolith

ageing is a time consuming process and requires specialized equipment, it can provide more accurate interpretations of age and is required for period calibration of statistical methods (Campana and Fowler, 2012). This project establishes a collection of aged silver hake otoliths and data at the Center for Fisheries Ecosystem Research that can be used for future reference. Further research could employ these otoliths to investigate origins of silver hake in the Gulf using otolith microchemistry methods and could explore whether this trend is supported by reproduction within the Gulf or by constant migration from nearby regions.

My research did not set out to predict future trends for silver hake in the Gulf, however it appears that the conditions faced by this species at its new range edge may be tempering its population expansion. The Gulf is an ecosystem that is undergoing major shifts in environmental (Stortini et al., 2016; Galbraith et al., 2018) and biological (Bourdages et al., 2018) conditions. The warming of the deep layer of the Gulf, which is hypothesized to be the main driver of the silver hake expanding range into the region, is a part of the natural variability in current interactions in the Northwest Atlantic (Brickman et al., 2018). The future trend of silver hake's abundance in the Gulf will likely depend on whether the current warming trends persist. My research has quantified silver hake biology at an early stage in their potential establishment in the Gulf, and provides results and physical records that can be compared with in future assessments of this species. Silver hake has the potential to impact resident species as well as become an emerging fishery, and continued monitoring of this species in the Gulf is necessary.

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Appendix A: Figure pertaining to diet complexity of silver hake in the Gulf of St. Lawrence

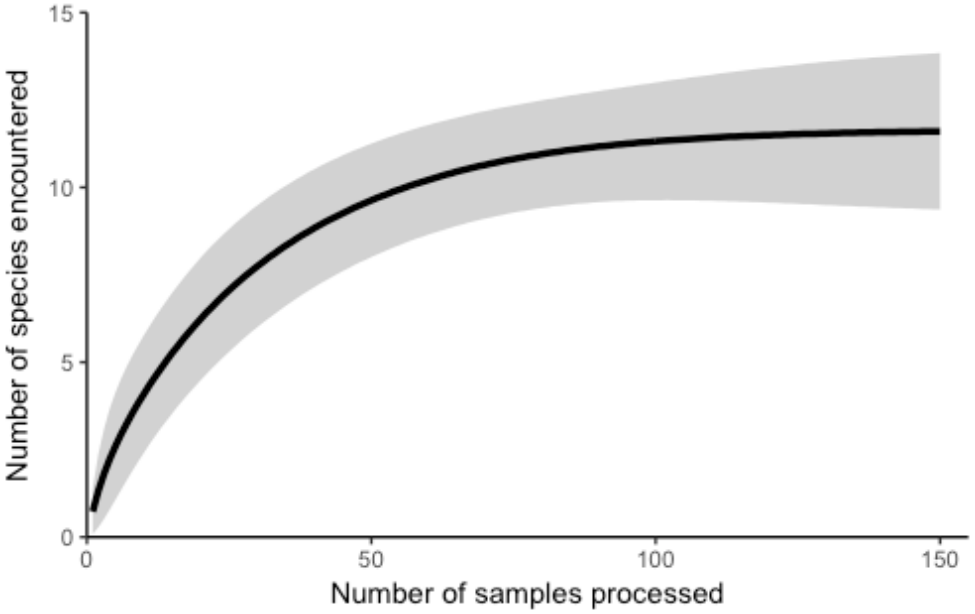

Figure A1: Species accumulation curve generated from the sample of 90 silver hake stomachs. Based on the curve, 66 samples are required to reach 90% of the asymptotic value.

Appendix B: Figures pertaining to the accuracy tests performed using silver hake otolith training sets

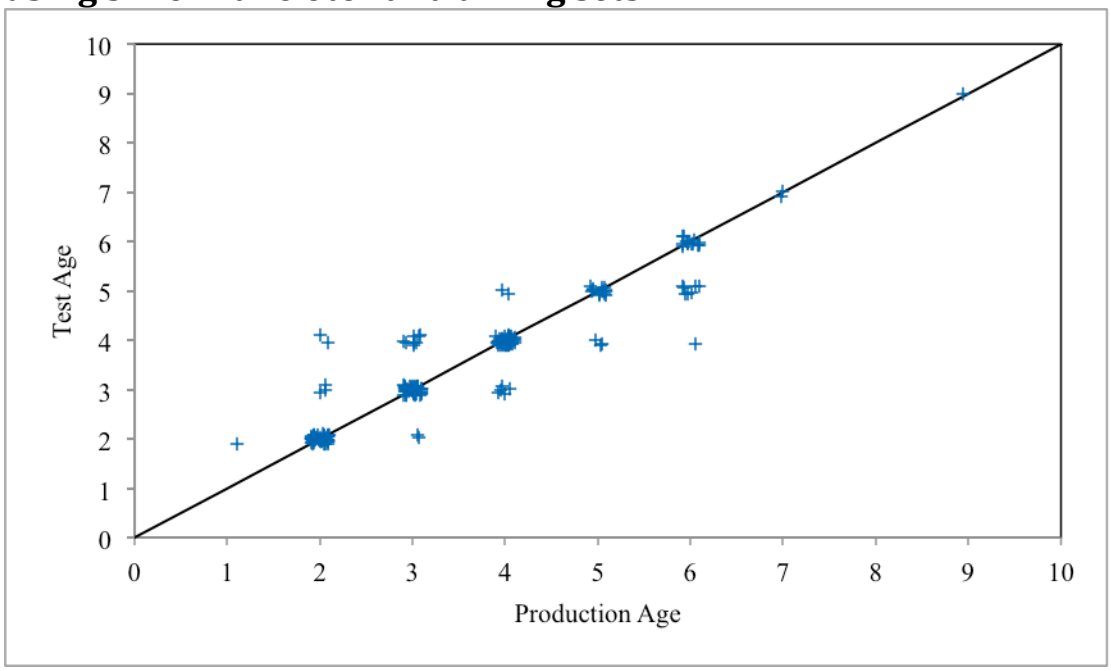

Figure B1: Tested ages plotted against production ages (as aged by NEFSC staff) for the precision test set using Q3 commercial samples. A percentage agreement of 82.7% and a coefficient of variation of 3.77% were achieved.

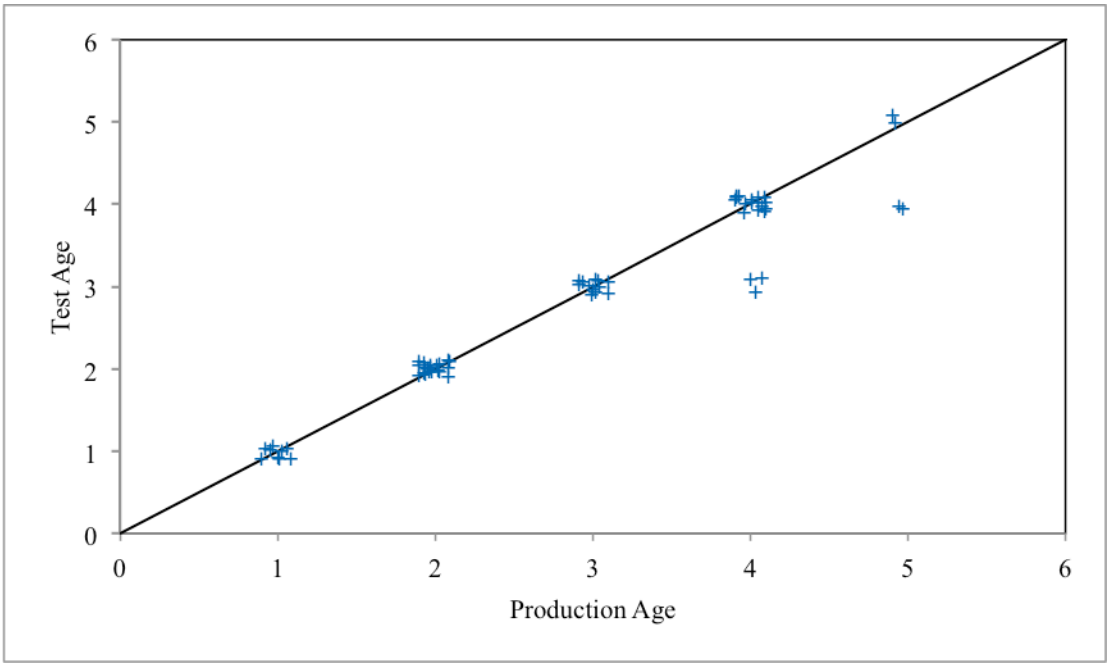

Figure B2: Tested ages plotted against production ages (as aged by NEFSC staff) for the precision test set using Q3 survey samples. A percentage agreement of 92.3% and a coefficient of variation of 1.42% were achieved.